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AMERICAN NATURALIST

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A GENETIC ANALYSIS OF THE CHANGES PRODUCED BY SELECTION IN EXPERIMENTS WITH TOBACCO[1]

PROFESSOR E. M. EAST AND H. K. HAYES

BUSSEY INSTITUTION OF HARVARD UNIVERSITY

THE PROBLEM

IN 1903 Johannsen announced that continued selection of the extreme values of certain quantitative characters in successive self-fertilized generations of a number of strains of beans had produced no changes in the mean values of the characters. He concluded that these particular strains were homozygous for the gametic factors whose interaction resulted in the characters investigated, that these homozygous characters may be properly described by one or more gametic factors nonvariable in transmissible qualities and properties, and that the variations observed in the characters of any single fraternity were due entirely to the action of environmental conditions during ontogeny and were not inherited. Fundamentally, these conclusions were a recognition of the general value of Mendelian description for all forms of inheritance through sexual reproduction, combined with an

[1] These investigations were conducted with funds furnished by the Connecticut Agricultural Experiment Station from their Adams' appropriations, by the Bureau of Plant Industry of the United States Department of Agriculture, and by the Bussey Institution of Harvard University, and the writers desire to take this opportunity of expressing their sincere appreciation of this hearty cooperation which made the work possible.

admission of disbelief in the inheritance of ordinary adaptive changes. The latter conception was Weismannian in that all inherited variations were held to be changes in the germ cells. It was not necessary to suppose it impossible for the environment to produce such changes and therefore to have been of no value during the course of evolution, but merely to suppose that during the comparatively short period of experimental investigations no gametic variations have occurred traceable to such a cause. For his first conclusion to be justified, it was assumed that the changes which every biologist knows do follow the continuous selection of extremes under certain conditions are to be interpreted entirely by the segregation and recombination of hypothetical gametic factors which are constant in their reactions under identical conditions.

Numerous investigators working on "pure lines" with different material corroborated Johannsen's conclusions, and, as it was seen to be possible to interpret in the same manner changes made by selection in experiments where self-fertilized lines were not used, such as those of the Vilmorins and others on sugar beets and those of the Illinois Agricultural Experiment Station on maize, many biologists accepted them and considered them a great advance over former conceptions of the mechanism of heredity. On the other hand, there were those who maintained a skeptical attitude, the chief criticism directed against the conception being that all progress due to selection must have a limit, which in many of these experiments had already been reached, and that even if results were being obtained action might be too slow to be detected.

The Material

These criticisms were reasonable when applied to certain specific cases, and in 1908 the experiments reported in this paper were designed with the hope of testing their validity, using the species ordinarily grown for commercial tobacco, *Nicotiana tabacum,* as the material. This plant satisfies the conditions which are requisite for

material used in pure line studies. It has characters that can be estimated readily and accurately and which are affected only slightly by external conditions. It is easily grown, is naturally self-fertilized, reproduces prolifically, and is known in many markedly different varieties. In fact, it is an ideal subject for work of this kind.

The investigations were not patterned after the standard type set by Johannsen wherein the constancy of successive generations of pure lines grown from selected extremes were tested, since even if it were possible to gather a quantity of data at all comparable to that collected by Johannsen (:09) and Jennings (:08) in their brilliant investigations, the criticisms mentioned above might still be made. The plan chosen was that of crossing two varieties of tobacco which differed in a character complex easily and precisely determined, and of selecting extremes from a number of families of the F_2 generation. If Johannsen's views be incorrect, such continued selection should affect each family in the same degree. If his conclusions be justified, selection should reach an end-point in different generations in different families, and there should be no relation between the number of generations required to reach this end-point and the progress that is possible.

There should be no need of a historical summary of the previous investigations that have been interpreted as corroborating or refuting Johannsen's conclusions. Such summaries have been made in other papers. It should be mentioned, however, that the classical researches of Pearl (:11) on the inheritance of fecundity in the domestic fowl have been so planned and executed that certain of the criticisms directed against Johannsen mentioned above are not justified, yet Pearl finds himself thoroughly in accord with the Danish physiologist's position.

Several hundred varieties of *Nicotiana tabacum* exist which differ from each other by definite botanical characters, yet only two general characters suitable for our purpose were found. We desired to confine our observations to quantitative characters that were influenced but

little by environment, and number of leaves and size of corolla were the only ones that satisfied this requirement. Such character differences as height of plant and size of leaf, while undoubtedly transmissible, are influenced so strongly in their development by nutrition that work with them is exceedingly difficult. For example, if a certain variety of *Nicotiana tabacum* is grown under the best of field conditions, the longest leaves are about 28 inches and the total height about 6 feet, but a portion of the same seed fraternity may be grown to maturity in 4-inch pots without reaching a height of over 16 inches or having leaves longer than 4 inches. On the other hand, several experiments conducted in the same manner have shown no difference between the frequency curves of variation in number of leaves or of size of corolla, whether starved in small pots or grown under optimum conditions. The character complex number of leaves was chosen for this investigation rather than the size of corolla because varieties that differ greatly in number of leaves are common.

TABLE I

Frequency Distribution of Number of Leaves per Plant when Starved in Small Pots

(Compare with frequency distribution under normal field conditions at Forest Hills, Massachusetts, in Tables VII and XI)

Plant No.	No. of Leaves per Plant															
	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
(6–1)	...	2	3	10	15	8	7	1	...	...	...	...	...	...	...	...
(6–1)–1	...	1	6	8	15	16	12	5	...	...	...	...	...	...	...	...
(6–2)	...	...	...	1	0	8	7	14	15	14	8	3	3	...	...	...
(6–2)–2	...	...	...	...	1	0	1	0	2	3	12	17	16	8	0	1
(56–1)	...	1	4	8	12	6	7	2	...	...	...	...	...	...	...	...
(56–2)	...	...	...	4	6	10	13	8	3	1	...	...	...	...	...	...

Previous Work of the "Havana" × "Sumatra" Cross

Several crosses have been made between varieties of tobacco that had a mean difference of seven or eight leaves, but the majority of the data reported here were collected from the descendants of a cross made by A. D. Shamel between the types known in Connecticut as "Havana" and "Sumatra." The "Havana" parent was

from a variety that had been grown for a number of years at Granby, Connecticut. It averages about 20 leaves per plant although ranging from 16 to 25 leaves. The average height is about 1.4 m. and the average leaf area about 7 sq. dm. The "Sumatra" parent was a type specimen of a variety that had been introduced into Connecticut to be grown under cloth shade. It averages between 26 and 27 leaves per plant with a range of from 21 to 32 leaves. The average height is nearly 2.0 m., but the average leaf area is only about 3 sq. dm.

According to Shamel, the first hybrid generation of this cross developed somewhat more vigorously than the parent types and was uniform in its habit of growth. The second generation, he thought, was hardly more variable than the first. Several F_3 families, the progeny of inbred F_2 individuals, were grown in 1906 and proved to be a variable lot. One of these plants produced 26 small, round-pointed leaves with short internodes between them. This plant was thought by Mr. E. Halladay, upon whose farm the experiment was conducted, and Mr. J. B. Stewart, of the U. S. Department of Agriculture, to be worth saving from its promise of producing a desirable commercial type.

In 1907 the Department of Agriculture made an agreement with Mr. Halladay to grow two acres of tobacco for experimental purposes, and on his own initiative Mr. Halladay grew a number of plants from inbred seed of the one that bore 26 leaves. This selection, numbered 2 h-29 in accordance with the department nomenclature, was comparatively uniform in appearance and several plants were selfed. In Mr. Halladay's absence, however, all of the plants were "topped," except one that happened to be rather late. This plant was selfed. It had 26 medium-sized, round leaves and grew to about the same height as the Connecticut Havana.

In view of Mr. Halladay's high opinion of the type, the seed of this plant and the remaining seed of its parent were planted in 1908. The plants of this generation presented a uniform appearance and promised a high grade

of wrapper tobacco, but the crop when cured lacked uniformity. Some leaves of exceptionally high quality were produced, but the crop in general lacked that characteristic known as "grain" and had too large a proportion of heavy leaves—the so-called "tops."

From this 1908 generation 100 seed plants were selfed, their leaves harvested, cured and fermented separately, and data on quality recorded. The type was also grown commercially on a large scale. The commercial results, however, have been reported in another paper. We are to consider only the results of the selection experiment that began in 1908, through the cooperation between the U. S. Department of Agriculture and the Connecticut Agricultural Experiment Station, a joining of forces that in 1909 included the Bussey Institution of Harvard University. Shamel (:07) considered the strain produced by this cross to be the result of a mutation. From a study of the data from the previous work on the cross it seemed to the writers that a different interpretation of the results might be made. While it was not impossible that the many-leaved type that had been isolated was the result of a mutation, it appeared much more probable that it had arisen through a recombination of Mendelian factors. The type had the habit of growth and size of leaf of the pure "Havana" variety and the number of leaves of the "Sumatra" variety, a combination that might reasonably be expected to be the result of the Mendelian law.

RESULTS ON THE RECIPROCAL CROSS, "SUMATRA" × "HAVANA"

To test the hypothesis that the new tobacco was the result of such recombination and could be reproduced whenever desired, the reciprocal of the original cross was made in 1910. The female parent, "Sumatra," was the direct descendant of a sister of the plant used as the male parent of the original cross by Shamel in 1903 through seven generations of selfed plants. The male parent, "Havana," was from the commercial field of the Windsor Tobacco Growers' Corporation at Bloomfield,

Connecticut. It was a descendant in a collateral line of the plant used by Shamel in 1903 as the female parent in his cross.

Table II, giving the frequency distribution for the number of leaves of the two parents and the first and the second hybrid generations, is a complete justification of our prediction as to how the hybrid type produced by Shamel originated. The "Sumatra" and the F_1 generation were grown at New Haven, Connecticut, in 1911, the "Havana" was grown at Bloomfield, Connecticut, in 1911 from commercial seed of the same variety as the plant used for the male parent, while the F_2 generation was grown at New Haven, Connecticut, in 1912. The F_1 generation, producing an average of $23.3 \pm .14$ leaves per plant, is intermediate in leaf number, since the "Havana" variety shows an average leaf number per plant of 19.8 $\pm .08$ and the "Sumatra" variety $26.5 \pm .11$. The variation as determined by the coefficient of variability is somewhat less for the F_1 than for either parent. The value for the "Sumatra" variety is 6.64 per cent. $\pm .28$ per cent., for the "Havana" variety 6.98 per cent. $\pm .27$ per cent. and for the F_1 generation 6.24 per cent. $\pm .41$ per cent. Taking into consideration the probable error in each case, one may say that the variability of the three populations is almost the same.

The variability of the F_2 generation, however, is greatly increased. This is shown by the high coefficient of variability, $10.29 \pm .23$ per cent., although a glance at the frequency distribution with its range of from 18 to 31 leaves brings home the point without recourse to biometrical calculation.

The appearance of the plants in the field corroborated the data of Table II in other characters. The F_1 generation was intermediate in the various leaf characters, such as shape, size and texture, that distinguish "Sumatra" from "Havana" tobacco, and in these characters it seemed as uniform as either of the parental varieties. On the other hand, the F_2 generation was extremely variable. Some plants could not be distinguished from the pure "Suma-

tra," others resembled "Havana," although of course the majority were intermediate in various degrees. Several plants combined the leaf size and habit of growth of the "Havana" parent with the leaf number of the "Sumatra" parent. *In other words, plants were produced in the F_2 generation by the recombination of Mendelian factors that exactly repeated the type which Shamel had obtained in the F_3 generation of the reciprocal cross made in 1903 and which he thought was due to a mutation.* This fulfilled adequately the prediction made by us in 1908.

Results of Selecting for High Number and Low Number of Leaves in the "Havana" × "Sumatra" Cross

In describing the reproduction of Shamel's hybrid with numerous large leaves by a reciprocal cross, there has been a chronological inversion. This was done simply to show that the original hybrid known commercially as "The Halladay" was actually a recombination of Mendelian factors in which the "Havana" and the "Sumatra" varieties differed. We will now describe the effects of selection on the original "Halladay hybrid."

It will be recalled that the selection experiment which is the principal subject of this paper began with the selfing of 100 seed plants of Shamel's Halladay hybrid in 1908. These plants were the F_4 and F_5 generations of the cross "Havana" × "Sumatra." Plants numbered from 1 to 49 were the F_4 generation; those numbered from 50 to 100 were the F_5 generation. They were apparently breeding true for the short habit of growth and large-sized leaf of the "Havana" parent and the goodly number of leaves of the "Sumatra" parent. The casual observer either would have said with Shamel that here was a mutation breeding as true as any tobacco variety, or that a fixed hybrid, a hybrid homozygous in all of its gametic factors, had been produced. Accurate data taken on the progeny of those of the F_4 and F_5 seed plants which it was possible for us to grow in our limited space,

however, show that such judgments would have been superficial. The general type of the plant did appear to be fixed, but the frequency distribution for number of leaves of the F_5 and F_6 populations were not the same. Strictly speaking, they were not fixed. What would be the result of selecting (and selfing) extremes from these different families for a number of years? A tentative answer to this question is to be obtained by examining the remainder of our tables.

The tables are arranged roughly in the order of the effect that selection has had in changing the mean of the various families that were the starting points of this part of the experiment. The selections were grown near Bloomfield, Connecticut, on the light sandy loam of that region, soil typical of that which produces the famous Connecticut River Valley wrapper tobacco. Duplicate experiments with several of the original families were made at New Haven, Connecticut, however, on an impoverished soil not fitted to grow a good quality of tobacco even after supplying large quantities of tobacco fertilizer, and in the condition used not fitted to grow good crops of any kind. Two families were also grown in triplicate, the third selections being planted at Forest Hills, Massachusetts, on a very fine type of rich garden land which brought out maximum luxuriance of growth, but which did not produce good tobacco quality. These experiments were not true repetitions of the experiments at Bloomfield, Connecticut, since aliquot portions of the seed from the selfed plant grown there were not sent to the other places to be grown. But they were duplicates in that each family came from the same F_4 or F_5 mother plant, although, beginning with the F_5 or F_6 population, different selfed seed plants furnished the starting point of selections carried on independently. In this way there were afforded a greater number of chances to see what selection could do.

Table III shows the results obtained from family No. 77. This family arose from an F_5 plant having 23 leaves, one below the modal leaf number if we may judge from

TABLE II

Frequency Distribution of Number of Leaves per Plant in Cross Between Havana (Female) and Sumatra (Male) Tobaccos

Variety	Number of Leaves per Plant															Total	A.	S. D.	C. V.
	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31				
Havana	3	22	44	42	22	10	6	1	...	...	...	...	...	...	...	150	19.8 ± .08	1.38 ± .05	6.98 ± .27
Sumatra	...	...	...	...	...	...	3	13	27	25	21	16	15	4	1	125	26.5 ± .11	1.76 ± .08	6.64 ± .28
Sumatra × Havana, F_1	...	...	...	2	4	9	14	15	5	2	1	...	...	...	...	52	23.3 ± .14	1.45 ± .10	6.24 ± .41
Sumatra × Havana, F_2	...	1	9	21	33	48	66	71	71	59	49	25	18	7	2	480	24.4 ± .08	2.51 ± .06	10.29 ± .23

TABLE III

Frequency Distribution of Number of Leaves in Family 77, Grown at Bloomfield, Conn.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant																				Total	A.	S. D.	C. V.
				14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33				
(77–1)–1–2	F_9	1912	20	1	3	16	46	67	58	31	6	4	2	1	1	...	...	...	...	...	...	...	...	236	18.4 ± .07	1.54 ± .05	8.37 ± .26
(77–1)–*1*	F_8	1911	20	...	...	...	...	2	20	68	97	65	32	14	6	2	...	...	...	...	...	...	...	306	21.3 ± .05	1.41 ± .04	6.60 ± .18
(77–1)	F_7	1910	20	...	...	...	1	5	20	49	53	47	37	20	21	9	2	2	...	...	...	...	...	266	21.9 ± .08	2.03 ± .06	9.27 ± .27
77	F_6	1909	23	...	...	...	...	...	...	10	12	24	23	10	5	0	1	...	...	...	...	...	...	85	22.4 ± .11	1.35 ± .07	6.38 ± .33
(77–2)	F_7	1910	27	...	...	...	...	...	...	4	11	15	34	35	39	30	27	15	6	5	2	1	...	224	24.9 ± .11	2.32 ± .07	9.32 ± .30
(77–2)–1	F_8	1911	30	...	...	...	...	...	...	...	...	2	10	24	38	68	59	41	21	12	4	1	1	281	26.6 ± .07	1.84 ± .05	6.92 ± .20
(77–2)–1	F_8	1912	30	...	...	...	...	...	...	...	1	5	25	44	50	62	43	29	12	3	4	1	1	280	25.8 ± .08	1.93 ± .06	7.48 ± .21

GROWN AT NEW HAVEN, CONN.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant																					Total	A.	S. D.	C. V.
				17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37				
(77-1)-1-1	F_9	1912	21	1	7	10	29	44	34	9	1	...	...	...	...	...	...	...	...	...	...	...	...	...	135	20.9 ± .08	1.29 ± .05	6.17 ± .25
(77-1)-1	F_8	1911	20	...	...	4	17	41	45	25	6	3	...	...	...	...	...	...	...	...	...	...	...	...	141	21.7 ± .07	1.22 ± .05	5.61 ± .23
(77-1)	F_7	1910	20	...	...	5	18	35	44	51	27	18	7	4	4	0	0	1	...	...	...	...	...	...	214	22.7 ± .09	1.90 ± .06	8.37 ± .27
77[3]	F_6	1909	23	...	...	...	10	12	24	23	10	5	0	1	...	...	...	...	...	...	...	...	...	...	85	22.4 ± .11	1.35 ± .07	6.38 ± .33
(77-2)	F_7	1910	27	...	...	...	1	1	10	31	33	37	32	23	13	10	2	3	2	2	1	...	...	...	201	25.4 ± .11	2.35 ± .08	9.25 ± .31
(77-2)-1	F_8	1911	28	...	...	...	...	...	3	7	12	20	27	31	23	13	6	2	...	...	...	...	...	...	144	26.5 ± .11	1.92 ± .08	7.23 ± .29
(77-2)-1-1[4]	F_9	1912	30	...	...	...	...	...	...	...	...	1	1	11	33	30	17	11	10	3	2	7	0	2	128	29.7 ± .14	2.29 ± .10	7.71 ± .04

TABLE IV

FREQUENCY DISTRIBUTION OF NUMBER OF LEAVES IN FAMILY 76, GROWN AT BLOOMFIELD, CONN.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant													Total	A.	S. D.	C. V.
				20	21	22	23	24	25	26	27	28	29	30	31	32				
(76-1)-1	F_8	1911	23	1	4	34	72	105	66	18	9	1	...	...	...	...	310	23.9 ± .05	1.26 ± .03	5.28 ± .14
(76-1)	F_7	1910	22	1	0	0	3	4	8	9	6	...	...	...	...	...	31	25.2 ± .19	1.53 ± .13	6.07 ± .52
76	F_6	1909	23	1	4	9	18	23	15	14	4	1	...	...	...	...	89	24.1 ± .11	1.60 ± .08	6.64 ± .34
(76-2)	F_7	1910	27	...	4	16	40	54	50	27	10	6	1	1	...	...	209	24.4 ± .07	1.53 ± .05	6.27 ± .21
(76-2)-1	F_8	1911	28	...	...	2	9	31	54	48	35	24	20	5	1	1	230	26.1 ± .08	1.80 ± .06	6.88 ± .22
(76-2)-1-1	F_9	1912	29	...	...	1	4	16	38	59	59	54	27	14	2	1	275	26.9 ± .07	1.69 ± .05	6.28 ± .18

[3] Grown at Bloomfield, Connecticut.

[4] A number of plants showed leaf doubling.

the F_2 generation of the reciprocal cross where the mode was at 24 to 25 leaves. The F_6 fraternity that it produced was somewhat smaller than one would wish if he were to be confident of the calculations made. The mode is 22 leaves and the mean nearly the same, 22.4 ± .11 leaves. From among these plants, a minus variant having 20 leaves and a plus variant having 27 leaves were selected to produce the F_7 generation. The modes in this generation are 21 and 25 leaves, respectively, a difference of 4 leaves; and the means are 21.9 ± .08 and 24.9 ± .11 leaves, respectively, a difference of 3 leaves. Progress in both directions continued when a 20-leaved plant was selected to carry on the minus strain, and a 30-leaved plant was selected to carry on the plus strain. The modal classes of the F_8 generation are 21 leaves in the minus selection and 26 leaves in the plus selection, while the means are 21.3 ± .05 leaves and 26.6 ± .07 leaves, respectively. In the F_9 generation the plus selection was lost, but the minus selection grown from a 20-leaved plant had the mode dropped to 18 leaves and the mean to 18.4 ± .08 leaves. In order not to lose the plus selection entirely, however, more of the F_8 generation seed was grown in 1912. The mode is the same as in 1911, but the mean dropped slightly to 25.8 ± .08 leaves.

Here one notices what is very common throughout the experiment; the extremes selected for mother plants were not members of the most extreme classes. This means simply that vigorous healthy specimens were always selected as the mother plants, and often the most extreme variants did not come up to the standard. It is hardly just to criticize this procedure, however, for with the best care that it was possible to give, the experiments with several families were terminated on account of non-germination of seed or for some similar reason, it being impossible, on account of the pressure of other work, to self many plants in each selection. Even where seed from several mother plants was collected, it did not insure the continuation of that selection. The necessary space and care involved in growing so many seedlings in

TABLE V

Frequency Distribution of Number of Leaves in Family 19, Grown at Bloomfield, Conn.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant																Total	A.	S. D.	C. V.
				21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36				
(19–1)–1	F_7	1911	24	1	3	13	30	42	46	25	16	7	4	1	1	1	...	...	...	190	25.8 ± .09	1.87 ± .07	7.26 ± .25
(19–1)	F_6	1910	24	...	...	3	19	26	41	53	43	26	12	2	2	...	...	...	...	227	26.9 ± .08	1.76 ± .06	6.54 ± .21
19	F_5	1909	26	1	4	6	12	23	29	34	24	12	2	...	...	...	...	...	...	147	26.3 ± .10	1.79 ± .07	6.81 ± .27
(19–2)	F_6	1910	29	...	...	...	3	5	18	24	28	46	28	12	7	5	1	1	1	179	28.7 ± .10	2.05 ± .07	7.14 ± .26
(19–2)–2	F_7	1911	30	...	...	...	1	2	10	24	39	41	51	23	14	5	2	...	...	212	29.2 ± .08	1.78 ± .06	6.11 ± .20

Grown at New Haven, Conn.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant																Total	A.	S. D.	C. V.
				17	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35				
(19–1)–1–1	F_8	1912	24	...	...	...	...	3	5	29	51	30	17	4	3	...	...	...	...	142	27.3 ± .08	1.32 ± .05	4.84 ± .19
(19–1)–1	F_7	1911	22	1	1	7	9	16	17	18	10	8	1	2	...	...	...	...	...	90	25.1 ± .15	2.08 ± .11	8.29 ± .42
(19–1)	F_6	1910	24	...	1	2	15	43	57	45	29	7	...	...	...	...	...	...	...	199	25.2 ± .06	1.33 ± .05	5.28 ± .18
19[5]	F_5	1909	26	...	1	4	6	12	23	29	34	24	12	2	...	...	...	...	...	147	26.3 ± .10	1.79 ± .07	6.81 ± .27
(19–2)	F_6	1910	29	...	...	...	...	7	25	34	47	46	22	7	2	...	...	...	...	190	27.1 ± .07	1.50 ± .05	5.54 ± .19
(19–2)–1	F_7	1911	29	...	...	...	...	...	2	14	21	27	17	16	7	3	0	1	...	108	28.3 ± .11	1.70 ± .08	6.01 ± .28
(19–2)–1–2	F_8	1912	32	...	...	...	...	1	1	4	9	19	30	36	31	12	7	6	4	160	30.0 ± .11	2.02 ± .08	6.73 ± .25

[5] Grown at Bloomfield.

isolated seed pans filled with sterilized soil made it impossible to start more than two sets of plants for each plus and each minus selection. Generally both sets grew perfectly, but occasionally both failed, and in that case it was usually too late in the season to start a third set even if it were available.

The second part of Table III shows the results obtained on the poor soil of New Haven, Connecticut, with the same family. There was continuous progress in both directions. The minus selections during the three generations show a constant reduction of mode, the figures being 23, 22 and 21; the plus selections show an even greater increase in mode, the figures being 25, 27 and 28. The same decrease and increase occur in the means until in the F_9 generation there is a difference of nearly 9 leaves, the calculated means being 20.9±.08 leaves and 29.7±.14 leaves, respectively.

Figs. 1 and 2 show typical plants of the plus and minus strains of this family as developed by 3 years of selection. Fig. 3 illustrates an interesting change of phyllotaxy in some plants of (77–2)–1–1 as grown at New Haven in 1912.

Passing to the data on Family No. 76 (Table IV) there is the same evidence of the effectiveness of selection, excluding the minus strain in 1910, of which only 31 plants were healthy. This effect is markedly less than with the other family. The mode of the minus selection remained at 24 leaves and the mean was reduced only from 24.1 ± .11 leaves to 23.9 ± .05 leaves,—hardly a significant figure. The mode of the plus selection crept up to 26–27 and the mean to 26.9 ± .07 leaves, there being here one more generation than in the case of the minus strain.

Table V gives the data on plus and minus selections of Family No. 19 at Bloomfield for two generations. The original family stock of the F_5 generation has the mode at 27 leaves and the mean at about 26 leaves. A 24-leaved plant of this generation became the parent of the minus strain, giving in the F_6 generation a population with the same mode and a slightly higher mean (26.9 ± .08 leaves). Continuation of the strain through a 24-leaved plant gave

an F_7 population with the mode one class lower and the mean at 25.8 ± .09 leaves. Whether this slight reduction really means anything we are unable to say. At least, if it yields at all to selection, the progress is very slow. On the other hand, a considerable gain has been made in the plus selections. The mode rose immediately to 29 leaves when the progeny of a 29-leaved plant were grown, and went up to 30 leaves the next generation, the modal condition being the same as the number of leaves of the parent plant. The means are 26.3 ± .10 leaves, 28.7 ± .10 leaves and 29.2 ± .08 leaves, the amount of progress being—as may be seen—2.4 leaves and 0.5 leaf in the two successive generations. This result apparently indicates a slowing down of the effect of selection.

FIG. 1. PLANT OF HALLADAY HAVANA TOBACCO (77-2)-1-1, WHICH AVERAGES 29.7 LEAVES PER PLANT. IT IS THE RESULT OF THREE YEARS OF SELECTION FOR HIGH LEAF NUMBER IN FAMILY 77, WHICH AVERAGED 22.4 LEAVES PER PLANT IN 1909. NEW HAVEN, 1912.

The continuation of the table gives the results obtained at New Haven on this same family. Here there are data from three generations, and these data modify the conclusions based on the results obtained at Bloomfield. Both plus and minus strains nearly parallel the Bloomfield results for two generations,

the F_7 generation means being 28.3 ± .11 leaves and 25.1 ± .15 leaves, respectively, but in the F_8 generations they differ. Selecting minus extremes for the first two genera-

FIG. 2. PLANT OF HALLADAY HAVANA TOBACCO (77-1)-1-1, WHICH AVERAGES 20.9 LEAVES PER PLANT. IT IS THE RESULT OF THREE YEARS OF SELECTION FOR LOW LEAF NUMBER IN FAMILY 77. NEW HAVEN, 1912.

tions reduced the mean of that line from 26.3 ± .10 leaves to 25.1 ± .15 leaves, but the third selected generation (F_8) had a higher mean than the original family (27.3 ± .08 leaves). The parent plant of this F_3 generation produced

24 leaves, and as the strain indicated that it was heterozygous for a number of factors by showing a coefficient of variability of 8.29 ± .42 per cent., it is possible that the selected parent plant may have belonged gametically to a higher class than was indicated somatically; nevertheless, it can not be denied that three generations of selected minus extremes have produced no results. This conclusion is not valid for the plus strain. Starting with 26.3 ± .10 as the mean number of leaves (F_5), the succeeding generations had means of 27.1 ± .07 leaves, 28.3 ± .11 leaves and 30.0 ± .11 leaves. The differences are 0.8, 1.2 and 1.7 leaves, respectively. Progressive change has certainly fol-

FIG. 3. CHANGE OF PHYLLOTAXY IN SOME PLANTS OF (77-2)-1-1 GROWN IN NEW HAVEN IN 1912.

lowed, and unless one considers that the results of 1912 are somewhat too high (probably a valid assumption), the change has increased instead of decreased. Naturally there must be a decreased momentum in change of mean time, but this decrease is not yet shown by the figures.

FIG. 4. PLANT OF HALLADAY HAVANA TOBACCO (19-2)-1-2, WHICH AVERAGES 30 LEAVES PER PLANT. IT IS THE RESULT OF THREE YEARS OF SELECTION FOR HIGH LEAF NUMBER IN FAMILY 19, WHICH IN 1909 AVERAGED 26.3 LEAVES PER PLANT. NEW HAVEN, 1912.

FIG. 5. PLANT OF HALLADAY HAVANA TOBACCO (19-1)-1-1, WHICH AVERAGES 27.3 LEAVES PER PLANT. THREE YEARS OF SELECTION FOR LOW LEAF NUMBER HAVE PROVED UNSUCCESSFUL. NEW HAVEN, 1912.

Representative plants of the plus and minus strains of family 19 as obtained by three years of selection at New Haven are shown in Figs. 4 and 5.

Family No. 5 (Table VI) shows a decrease in mode from 28 to 26 leaves, and a similar decrease in mean from 28.1 ± .06 leaves to 26.6 ± .09 leaves as a result of the first minus selection. A second minus selection, however, indicates either that the future progress is to be very slow or that the entire effect of selection was manifested in the first selected generation.

With the three parts of Table VII we take up the results on Family No. 6 at all three stations. The minus strain was carried on only two generations at Bloomfield, but with this exception there are data upon three generations. At Bloomfield the two generations of selected minus extremes resulted in 0.6 leaf decrease in the mean, but at New Haven the results were negative, the means advancing from 25.8 ± .06 leaves to 27.9 ± .12 leaves in three generations, while at Forest Hill the mean remained practically the same. Surely selection was unprofitable here.

The first year of selection from the other end of the curve, however, resulted in marked progress. The mean advanced nearly 5 leaves in each case. The original F_5 mean is 25.8 ± .06 leaves, but the three F_6 means are 30.7 ± .09, 29.6 ± .08 and 30.8 ± .12 leaves. This is a remarkable concurrence of results. The means in the two succeeding generations were about the same in the Bloomfield and New Haven experiments, but there was another definite advance at Forest Hills. Such a result should not be unexpected. If the F_6 generation were almost but not quite a homozygous lot, and if one assumes that selection of extremes from homozygous population has no effect in shifting the mean, it would frequently happen that some individuals selected to continue the line would be homozygous in all factors and some heterozygous in one or more factors.

The cause of the peculiar distribution of the population (high variability) of the F_8 generation grown in Bloom-

TABLE VI

FREQUENCY DISTRIBUTION OF NUMBER OF LEAVES IN FAMILY 5, GROWN AT BLOOMFIELD, CONN.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant														Total	A.	S. D.	C. V.
				21	22	23	24	25	26	27	28	29	30	31	32	33	34				
(5–1)–1	F_7	1911	24	...	...	3	14	35	71	68	38	5	3	1	1	...	...	239	26.5 ± .06	1.36 ± .04	5.13 ± .16
5–1	F_6	1910	25	2	0	2	24	31	52	45	23	16	8	6	1	1	...	211	26.6 ± .09	1.91 ± .06	7.18 ± .24
5	F_5	1909	28	...	...	1	3	5	26	67	73	72	29	15	2	1	...	294	28.1 ± .06	1.50 ± .04	5.34 ± .15
5–2	F_6	1910	31	...	...	...	...	1	7	26	43	55	46	26	15	4	3	226	29.2 ± .08	1.68 ± .05	5.75 ± .18
(5–2)–1	F_7	1911	32	...	...	...	5	5	13	37	54	53	46	20	8	1	1	243	28.6 ± .08	1.73 ± .05	6.05 ± .17
(5–2)–1–3	F_8	1912	33	...	...	1	2	4	20	32	42	63	63	31	18	5	1	282	29.0 ± .07	1.84 ± .05	6.34 ± .18

TABLE VII

FREQUENCY DISTRIBUTION OF NUMBER OF LEAVES IN FAMILY 6, GROWN AT BLOOMFIELD, CONN.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant																			Total	A.	S. D.	C. V.
				18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36				
(6–1)–2	F_7	1911	23	...	...	...	1	4	30	43	74	47	22	9	4	0	0	1	...	...	...	...	235	25.1 ± .07	1.52 ± .05	6.05 ± .19
(6–1)	F_6	1910	25	...	...	...	2	1	16	44	47	35	28	6	1	0	0	0	1	...	...	...	181	25.2 ± .08	1.53 ± .05	6.07 ± .22
6	F_5	1909	28	...	...	...	...	4	16	50	55	77	63	29	11	1	1	...	...	...	...	...	307	25.8 ± .06	1.59 ± .04	6.16 ± .17
(6–2)	F_6	1910	30	...	...	...	...	...	...	...	1	2	3	18	29	44	35	36	23	10	2	2	205	30.7 ± .09	1.90 ± .06	6.18 ± .21
(6–2)–1	F_7	1911	32	...	...	...	...	...	...	...	...	2	17	64	70	61	20	4	0	1	...	...	239	29.1 ± .05	1.21 ± .04	4.17 ± .13
(6–2)–1–4	F_8	1912	32	2	2	3	1	3	2	0	1	2	6	12	23	43	50	48	22	15	6	2	243	30.5 ± .13	3.03 ± .09	9.93 ± .30

Grown at New Haven, Conn.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant																		Total	A.	S. D.	C. V.
				21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38				
(6–1)–1–1	F_8	1912	25	...	3	5	12	16	26	31	21	12	17	3	2	...	...	...	...	...	...	148	27.9 ± .12	2.13 ± .08	7.63 ± .30
(6–1)–1	F_7	1911	23	1	5	10	24	36	36	14	9	1	1	1	2	...	...	...	...	...	...	140	25.4 ± .10	1.79 ± .07	7.06 ± .29
(6–1)	F_6	1910	25	...	1	10	41	42	41	32	14	11	2	1	...	...	...	...	...	...	...	195	25.7 ± .08	1.67 ± .06	6.50 ± .22
6[5]	F_3	1909	28	...	4	16	50	55	77	63	29	11	1	1	...	...	...	...	...	...	...	307	25.8 ± .06	1.59 ± .04	6.16 ± .17
(6–2)	F_5	1910	30	...	...	...	1	1	1	12	33	50	52	35	11	3	0	0	1	0	1	201	29.6 ± .08	1.63 ± .06	5.51 ± .19
(6–2)–1	F_7	1911	30	...	...	...	1	1	11	24	42	36	21	9	2	3	2	1	1	...	...	154	28.7 ± .10	1.84 ± .07	6.39 ± .24
(6–2)–1–1	F_8	1912	32	...	...	...	...	...	1	3	17	25	41	31	16	10	1	...	...	...	...	145	30.2 ± .09	1.51 ± .06	5.00 ± .20

Grown in Forest Hills, Mass.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant																		Total	A.	S. D.	C. V.
				22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39				
(6–1)–1–1	F_8	1912	24	...	3	14	34	56	28	13	4	...	...	...	...	...	...	...	...	...	...	152	26.0 ± .07	1.24 ± .05	4.77 ± .18
(6–1)–1	F_7	1911	26	...	1	5	19	31	55	31	9	1	1	...	...	...	...	...	...	...	...	153	26.8 ± .07	1.29 ± .05	4.81 ± .19
(6–1)	F_6	1910	25	...	2	14	23	29	15	8	2	...	...	...	...	...	...	...	...	...	...	93	25.8 ± .09	1.30 ± .06	5.04 ± .25
6[7]	F_5	1909	28	4	16	50	55	77	63	29	11	1	1	...	...	...	...	...	...	...	...	307	25.8 ± .06	1.59 ± .04	6.16 ± .17
(6–2)	F_6	1910	30	...	...	...	...	...	2	7	12	21	25	16	10	4	2	...	...	...	...	99	30.8 ± .12	1.70 ± .08	5.52 ± .27
(6–2)–2	F_7	1911	35	...	...	...	...	...	...	...	1	6	16	25	47	27	15	7	2	1	...	147	33.1 ± .09	1.54 ± .06	4.65 ± .18
(6–2)–2–2	F_8	1912	38	...	...	...	...	...	...	...	...	8	19	33	61	34	11	2	...	...	...	168	32.8 ± .07	1.27 ± .05	3.87 ± .14

[7] Grown at Bloomfield.

TABLE VIII

FREQUENCY DISTRIBUTION OF NUMBER OF LEAVES IN FAMILY 34, GROWN AT BLOOMFIELD, CONN.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant														Total	A.	S. D.	C. V.
				19	20	21	22	23	24	25	26	27	28	29	30	31	32				
(34-1)-2	F_7	1911	20	...	...	...	3	16	49	53	41	22	9	4	1	...	...	198	25.2 ± .07	1.47 ± .05	5.85 ± .20
(34-1)	F_6	1910	22	1	4	21	37	62	67	34	13	2	...	...	...	...	...	241	23.4 ± .06	1.43 ± .05	6.11 ± .19
34	F_5	1909	24	...	4	12	21	31	17	12	3	...	...	...	...	...	...	100	22.9 ± .09	1.40 ± .07	6.11 ± .29
(34-2)	F_6	1910	26	...	5	8	17	59	55	40	27	8	5	4	...	...	...	228	24.1 ± .08	1.72 ± .05	7.14 ± .23
(34-2)-2	F_7	1911	28	...	...	...	...	1	4	19	42	54	29	19	5	1	2	176	27.0 ± .08	1.48 ± .05	5.49 ± .20

TABLE IX

FREQUENCY DISTRIBUTION OF NUMBER OF LEAVES IN FAMILY 12, GROWN AT BLOOMFIELD, CONN.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant																Total	A.	S. D.	C. V.
				21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36				
(12-1)-1	F_7	1912	29	...	...	...	1	7	15	44	45	59	56	34	24	8	2	1	...	296	29.1 ± .08	1.94 ± .05	6.67 ± .19
(12-1)-1	F_7	1911	29	...	...	...	1	5	22	31	40	48	25	20	11	5	2	...	...	210	28.7 ± .09	1.93 ± .06	6.72 ± .22
(12-1)	F_6	1910	23	...	...	...	...	...	...	...	...	3	2	1	...	...	...	...	...	6	....	....	....
12	F_5	1909	24	6	7	17	23	24	27	8	1	...	...	...	...	...	...	...	...	113	24.5 ± .10	1.60 ± .07	6.53 ± .29
(12-2)	F_6	1910	28	1	5	16	30	37	39	28	25	19	13	1	1	...	...	...	...	215	26.1 ± .10	2.12 ± .07	8.12 ± .26
(12-2)-1	F_7	1911	30	...	...	2	11	21	50	54	41	13	4	1	1	...	...	...	...	188	26.8 ± .07	1.50 ± .05	5.61 ± .20
(12-2)-1	F_7	1912	30	...	...	1	3	6	9	23	39	58	43	34	6	8	0	0	1	231	29.0 ± .08	1.89 ± .06	6.52 ± .21

[6] Grown at Bloomfield.

field is not clear. It is possible that the plants having from 18 to 23 leaves were diseased, but no such condition could be recognized in the field. Again, it is possible that a few Havana plants were mixed in by mistake, although as the leaves of the selection are characteristically different from Havana and as the plants with low leaf numbers resembled the remainder of the row, this supposition is improbable. The most likely explanation is that mutation occurred in a few gametes of the mother plant, a condition that did arise, or that we assume to have arisen, in Family 41 (see Table X). At any rate, *the change did not follow the path of selection.*

In Figs. 6 and 7 are shown typical plants of Family No. 6 obtained by three years of selection in the effort to produce strains of high and low leaf number, respectively.

Family No. 34 (Table VIII) is peculiar—although this is not the only time the phenomenon occurred—in that the F_5 population grown from a 24-leaved F_4 plant seems not to have given the true mean. Plants with a low number of leaves (22 and 20) were selfed to carry on the minus strain, but both gave means higher than was shown by the F_5 generation. Perhaps further selection will produce results, but the case is not a hopeful one. The only evidence for such an assumption is the increased mean of the F_7 plus strain. If it is assumed that 24.0 is nearer the true mean of the F_5 population than the 22.9 actually calculated, then the jump to $27.0 \pm .08$ leaves in the F_7 generation gives us a basis for expecting results in F_8 in the minus strain.

Nothing can be said as yet about the minus strain of Family No. 12 (Table IX), for it happened that the first selection was a complete failure. Six plants were obtained, but the lowest number of leaves was 29. One of these plants was selfed and gave an F_7 population having a mean of $28.7 \pm .09$ leaves. Unfortunately the selections from this fraternity did not germinate and in 1912 we had to fall back on the reserve seed from which the 1911 crop came. The crops of 1911 and 1912 are therefore duplicates. The plus strain made an advance from $24.5 \pm .10$

leaves to either 26.8 ± .07 or 29.0 ± .08 leaves. The first advance is 1.6, the second 0.7. We can give no explana-

Fig. 6. Plant of Halladay Havana Tobacco (6-2)-1-1, which Averages 30.2 Leaves Per Plant. It is the Result of Three Years of Selection for High Leaf Number in Family 6, which Averaged 25.8 Leaves Per Plant in 1909. New Haven, 1912.

tion of the failure of the results of 1911 and 1912 to duplicate. This is the greatest deviation obtained in the course of our experiments. The results of 1912 are probably too high. It is yet too early to say whether or not this

FIG. 7. PLANT OF HALLADAY HAVANA TOBACCO (6-1)-1-1, WHICH AVERAGES 27.9 LEAVES PER PLANT. THREE YEARS OF SELECTION TO DECREASE THE LEAF NUMBER OF THIS TYPE HAVE PROVED UNSUCCESSFUL. NEW HAVEN, 1912.

strain is decreasing in the average annual shift of the mean.

Family No. 41 shown in Table X gave perhaps the most peculiar results of any of the selections. It may be that no great shifting of the mean toward the minus end of the curve should have been expected, because the minus mothers were each rather high in number of leaves. There was one with 25 leaves and one with 24 leaves. This was unfortunate, but was made necessary by the number of late and diseased (mosaic) plants in the selection. Nevertheless, each of these plants was below the mean of the previous generation and if a marked change would have followed the selection of extreme individuals, some change should have followed the selections of the individuals that were the actual mothers. But in spite of this fact the mean persistently rose from 23.9 ± .07 leaves to 26.3 ± .08 leaves, then to 28.1 ± .07 leaves, although the duplicate of this selection grown in 1912 went down slightly to 27.4 ± .07 leaves. In the plus strain successive generations of mothers having 28 and 30 leaves caused a small upward shift of the mean; it became first 25.7 ± .09 leaves then 25.6 ± .14 leaves, although the 1912 duplicate of the last population had a mean of 26.9 ± .08 leaves.

The extraordinary phenomenon to which we wish to call particular attention, however, is not this behavior of the minus and plus strains in the regular selection experiment, but rather the origin of a few-leaved strain from a single individual that appeared in the F_6 generation of the plus strain. Referring to the table, it will be seen that in this generation a 12-leaved plant appeared. This is really a peculiar phenomenon, for we had never before observed a normal 12-leaved plant among the many thousands that have come under our observation. They do not occur. In this population the plant with the next lowest numbers of leaves had 20 leaves, and in classes 20 and 21 there was only a single plant of each. This 12-leaved plant was selfed and gave rise to a population ranging from 8 leaves to 30 leaves, and having a variability of 23.50 per cent. ± .11 per cent. The mean of the

distribution was 19.8 ± .28 leaves. A 10-leaved plant of this lot was selfed and gave a progeny with a mean of 17.9 ± .08 leaves and a variability of 11.24 per cent. ± .33 per cent. What interpretation can be given these facts?

We believe a distinct mutation occurred, a mutation different from those of DeVries. At least DeVries believes that the mutations that he has observed always breed true. If the following hypothesis as to the origin of the 12-leaved plant be true, it is unnecessary to suppose with DeVries that mutations always breed true or even that they often breed true. Of course DeVries believes that his *Œnothera* mutations obey laws different from those of whose mechanism we know a little. He believes that species crosses always breed true; that they do not Mendelize. This belief we hold to be unfounded. Species crosses have never been shown to breed true. There have been statements to the effect that crosses between *Rubus* species breed true, but no good evidence has been submitted in their support; while the data of Tammes (:11) on *Linum* species crosses, Davis (:21) on *Œnothera* species crosses, and of East (:13) on *Nicotiana* species crosses, concur in showing that species as well as varieties obey Mendel's Law of segregation and recombination. Furthermore, we think that Heribert-Nilsson's (:12) beautiful experiments on DeVries's own material show that the latter did not collect sufficiently exact data on his own crosses to find out whether they bred true or not.

If one is to believe that a mutation in a hermaphroditic plant breeds true he must suppose that constitutional changes occur both in the male and the female gametes, or that the change occurs after fertilization. But it seems more probable that such a change will take place either in the one or the other gamete and not in both. This we believe to be the explanation of the appearance of the 12-leaved tobacco plant. A mutation occurred in either an egg cell or a pollen cell. It does not matter in which one it is assumed because there is no evidence favoring either case to the exclusion of the other. *This cell with*

TABLE X

Frequency Distribution of Number of Leaves in Family 41, Grown at Bloomfield, Conn.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant																								Total	A.	S. D.	C. V.
				10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33				
(41-1)-2	F_7	1912	25	..	..	..	..	..	..	..	..	..	..	..	..	4	3	8	17	51	74	62	36	24	6	3	..	288	27.4 ± .07	1.76 ± .05	6.42 ± .18
(41-1)-2	F_7	1911	25	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2	7	30	47	52	45	25	10	7	..	225	28.1 ± .07	1.64 ± .05	5.85 ± .19
(41-1)	F_6	1910	24	..	..	..	..	..	..	..	..	..	..	..	2	2	16	10	33	54	57	25	21	4	..	..	..	224	26.3 ± .08	1.75 ± .06	6.65 ± .21
41	F_5	1909	26	..	..	..	..	..	..	..	..	..	2	10	15	24	66	65	64	36	11	2	1	..	..	..	..	296	23.9 ± .07	1.71 ± .05	7.25 ± .20
(41-2)	F_6	1910	28	..	..	1[10]	..	..	..	..	..	..	..	1	1	4	24	36	42	44	41	21	13	7	..	..	..	234	25.7 ± .09	1.92 ± .06	7.47 ± .23
(41-2)-1[8]	F_7	1911	30	..	..	..	..	..	..	..	..	1	3	5	3	2	6	13	24	37	25	10	7	2	3	1	..	142	25.6 ± .14	2.49 ± .10	9.71 ± .39
(41-2)-3[9]	F_A	1911	12	5	3	3	3	5	3	0	8	8	8	21	8	14	6	9	8	7	4	0	0	1	..	..	..	126	19.8 ± .28	4.65 ± .20	23.50 ± .11
(41-2)-1	F_7	1912	30	..	..	..	..	..	..	..	..	..	..	2	1	3	10	16	39	54	60	59	35	21	5	4	1	310	26.9 ± .08	2.07 ± .06	7.70 ± .21
(41-2)-3-2	F_B	1912	10	..	1	0	3	5	24	37	60	51	54	17	20	3	1	0	1	0	1	..	..	..	..	..	..	278	17.8 ± .08	2.00 ± .06	11.24 ± .33

TABLE XI

Frequency Distribution of Number of Leaves in Family 56, Grown at Bloomfield, Conn.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant														Total	A.	S. D.	C. V.
				19	20	21	22	23	24	25	26	27	28	29	30	31	32				
(56-1)-1-3	F_9	1912	24	...	...	...	1	3	3	6	8	3	1	...	...	...	...	25	25.2 ± .19	1.44 ± .14	5.71 ± .55
(56-1)-1	F_8	1911	23	...	...	2	9	31	48	64	35	20	7	2	2	...	...	220	24.9 ± .07	1.57 ± .05	6.31 ± .20
(56-1)	F_7	1910	23	...	1	3	10	33	59	44	34	21	6	2	...	...	...	213	24.7 ± .07	1.59 ± .05	6.44 ± .21
56[11]	F_6	1909	26	1	4	13	31	49	79	72	43	19	2	2	...	...	...	315	24.2 ± .06	1.66 ± .05	6.86 ± .18
(56-2)	F_7	1910	28	...	...	...	...	2	19	23	51	48	28	24	8	2	...	205	26.7 ± .08	1.65 ± .06	6.18 ± .21
(56-2)-1	F_8	1911	27	...	...	1	0	2	10	28	57	60	41	27	6	...	...	232	26.8 ± .07	1.50 ± .05	5.60 ± .18

[8] This was an end row and the plants were very yellow and small, due to insufficient soil fertility.

[9] Also, one each bearing eight and nine leaves.

[10] Not used in computations.

[11] Three Havana plants were found in this row which bore 16, 18 and 21 leaves respectively. These were not used in computations.

GROWN AT NEW HAVEN, CONN.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant 19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	Total	A.	S. D.	C. V.
(56–1)–1–1	F_9	1912	23	...	...	...	2	34	45	34	21	6	2	...	...	...	...	...	...	...	144	24.4 ± .07	1.23 ± .05	5.04 ± .20
(56–1)–1	F_8	1911	24	...	1	5	18	36	46	28	14	8	2	...	...	...	...	...	...	...	158	24.0 ± .08	1.50 ± .06	6.26 ± .24
(56–1)	F_7	1910	23	...	...	...	5	26	47	47	46	24	16	6	...	...	...	...	...	...	217	25.2 ± .07	1.61 ± .05	6.39 ± .20
56[12]	F_6	1909	26	1	4	13	31	49	79	72	43	19	2	2	...	...	...	...	...	...	315	24.2 ± .06	1.66 ± .05	6.86 ± .18
(56–2)	F_7	1910	28	...	...	...	...	1	3	23	28	42	42	33	10	5	...	...	...	...	187	27.4 ± .08	1.60 ± .06	5.84 ± .20
(56–2)–1	F_8	1911	28	...	...	...	...	5	22	23	34	29	20	10	4	2	1	0	0	1	151	26.4 ± .11	1.93 ± .08	7.32 ± .28
(56–2)–1–2	F_9	1912	30	...	...	...	...	1	7	14	23	24	30	21	12	5	4	1	...	...	142	27.5 ± .11	1.97 ± .08	7.16 ± .29

GROWN AT FOREST HILLS, MASS.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant 19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	Total	A.	S. D.	C. V.
(56–1)–1–1	F_9	1912	23	...	...	...	2	5	27	44	45	27	18	5	5	...	...	...	...	178	25.9 ± .08	1.59 ± .06	6.14 ± .22
(56–1)–1	F_8	1911	23	...	...	...	1	1	12	31	59	34	10	3	...	...	...	...	...	151	26.0 ± .06	1.17 ± .05	4.50 ± .17
(56–1)	F_7	1910	23	...	...	...	2	7	16	26	36	10	4	...	...	...	...	...	...	101	25.3 ± .09	1.27 ± .06	5.01 ± .24
56[13]	F_6	1909	26	1	4	13	31	49	79	72	43	19	2	2	...	...	...	...	...	315	24.2 ± .06	1.66 ± .05	6.86 ± .18
(56–2)	F_7	1910	28	...	...	...	...	...	1	7	19	40	27	7	3	...	...	...	...	106	27.2 ± .08	1.16 ± .05	4.26 ± .20
(56–2)–2	F_8	1911	32	...	...	...	...	...	...	1	5	19	30	51	24	13	5	1	...	149	28.9 ± .08	1.42 ± .06	4.91 ± .19
(56–2)–2–2	F_9	1912	31	...	...	...	...	...	7	17	37	58	28	6	1	...	...	...	...	154	26.7 ± .06	1.18 ± .05	4.42 ± .17

[12] Grown at Bloomfield.

[13] Grown at Bloomfield.

a changed gametic constitution,—a loss of gametic factors,—was fertilized by an unchanged cell. The unchanged cell may have had any of the gametic possibilities open to the germ cells of the 28-leaved plant of the F_5 family in which the mutation arose, and we know that certain factors in this plant were heterozygous, for progressive change followed the selection of a plus extreme in the next generation. The 12-leaved plant was therefore a hybrid. It resulted from the union of a mutating germ cell of the mother plant that furnished the F_6 generation with an unchanged germ cell. We can even assume that the mutating germ cell, if fertilized by another of the same kind, would have produced a plant with less than 12 leaves. The reasons for believing this are simple. There is experimental evidence (Hayes, 1912) that the F_1 generation of a cross between varieties differing in their number of leaves is intermediate in character. Our 12-leaved plant is the lone representative of such an F_1 generation. The F_2 generation therefore should give plants with less than 12 leaves, and in fact such plants did occur. The distribution marked F_A in the table is the F_2 generation, and this accounts for its extreme variability. The distribution marked F_B is the F_3 generation, and its variability is less than half that of the preceding generation.

Family No. 56 was the second family to be grown at all three of the experimental stations (Table XI). It arose from a 26-leaved plant of the F_5 generation which produced an F_6 progeny with a mean of $24.2 \pm .06$ leaves and a mode at 24 leaves. The three generations of the minus strain grown at Bloomfield remained practically the same. The last generation did indeed show a mean 1.0 leaf higher than the original population, but no dependence can be placed in data from only 25 plants. The data on the minus selections grown at New Haven are for this reason a little more dependable. They show a fluctuating mean, but no progress due to selection, the F_9 generation having a little higher mean than the F_6 generations. The three minus selections grown at Forest Hills also

resulted in higher means, those for F_7, F_8 and F_9 being $25.3 \pm .09$, $26.0 \pm .06$ and $25.9 \pm .08$ leaves, respectively.

This peculiar result implies only that the mean of the original F_6 population which was grown at Bloomfield was lower than it would have been if grown on the Forest Hills' soil. This is not a direct effect of environment on the growing plant. It has been shown conclusively in our pot experiments, as stated before, that starvation or optimum feeding has scarcely any effect on the number of leaves, although it has a marked effect on the development of many other characters. On the other hand, environment does appear to have a marked effect on the number of leaves that a plant is to develop, if it acts *during the development of the seed.* It is well known by plant physiologists that the environment produces many of its effects very early in the life history of the individual or in the development of the organ concerned. For example, the so-called light leaves of the beech with two layers of palisade cells are differentiated from the shade leaves with only one row of palisade cells by the amount of light that falls on a branch during the season preceding the development of the leaves: that is, it is determined during the laying down of the bud from which the next season's growth of twig and leaves comes. This period during which a particular change is possible is called the critical period for that change by plant physiologists. Thus a plant may have hundreds of critical periods in its ontogeny, each marking an end-point of development beyond which a certain feature is irrevocably fixed. For example, the critical period for that cell division that determines leaf size in the beech is much later than that which determines the number of layers of palisade cells.

Now the critical period for influencing the number of leaves of the tobacco plant is practically at an end when the embryo plant goes into the resting stage of the seed. Before that time the number of leaves may be influenced by the external and the internal influences that form the total environment of the mother plant; after that time environment has little influence on the number of leaves.

The rise in the mean of the population of the F_8 generation of Family No. 56 is due partially to the effect of environment, therefore, in that the mother plant was grown under better conditions, but is probably not to any great extent due to the conditions under which the plants themselves were produced.

The better environment of the mother plants does not account for all the rise in the means in populations F_8 and F_9, but it accounts for part of it. It will be noticed that all of the populations grown at Forest Hills had higher means than those grown at Bloomfield and New Haven, although the F_6 mother plants were grown at Bloomfield and not at Forest Hills. The greatest shift of the mean, however, comes in the F_8 and F_9 generations, for the mother plants of both of these populations were grown on the more fertile soil. There is a simple explanation of these facts, an explanation that is of great economic importance to practical tobacco growers. A part of the rise in mean at Forest Hills was due to setting the plants in the field there when they were in an earlier stage of development than those at Bloomfield and New Haven. They were not set earlier in the season (at least, one year they were set early, one year they were set at the average time and the third year they were set late), but they were set as small plants. When small plants (about 4 inches high) are set in the open the root system is equal to the task of supporting the aerial parts and the plants start right in to growing normally. There is no period of passivity. The plants produce leaves spaced with normal internodes and these leaves develop sufficiently to have a commercial value. But when the plants reach a height of 8 or 10 inches in the seed pans or seed beds and are then set in the field, the normal metabolism is likely to be upset for a time. The plant takes some time to recover its equilibrium and start a normal growth. During this period basal leaves begin to develop, but the internodes are so close together that they do not obtain their aliquot share of nutriment, hence they grow only to one quarter or one third their normal size and soon wither

and drop off. The leaf scars are left, but they are so close together that it is difficult to make a correct count of the number of leaves. But more important than this,

FIG. 8. PLANT OF HALLADAY HAVANA TOBACCO (56-2)-1-1, WHICH AVERAGES 27.5 LEAVES PER PLANT. IT IS THE RESULT OF THREE YEARS OF SELECTION FOR HIGH LEAF NUMBER IN FAMILY 56, WHICH IN 1909 AVERAGED 24.2 LEAVES PER PLANT. NEW HAVEN, 1912.

FIG. 9. PLANT OF HALLADAY HAVANA TOBACCO (56-1)-1-1, WHICH AVERAGES 24.4 LEAVES PER PLANT. THREE YEARS OF SELECTION FOR LOW LEAF NUMBER HAVE PROVED UNSUCCESSFUL, NEW HAVEN, 1912.

TABLE XII

Frequency Distribution of Number of Leaves in Family K, Grown at Bloomfield, Conn.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant														Total	A.	S. D.	C. V.
				17	18	19	20	21	22	23	24	25	26	27	28	29	30				
(K–1)–1–2	F_8	1912	24	2	2	15	42	55	43	26	15	6	2	0	1	...	...	209	21.5 ± .08	1.67 ± .06	7.77 ± .26
(K–1)–1	F_7	1911	22	...	...	...	3	14	39	52	46	28	16	2	1	1	...	202	23.5 ± .07	1.53 ± .05	6.52 ± .22
(K–1)	F_6	1910	20(?)	...	...	...	...	7	13	25	34	32	23	9	3	2	...	148	24.4 ± .09	1.69 ± .07	6.93 ± .27
K	F_5	1909	26	...	...	...	2	4	10	12	3	...	...	...	...	...	...	31	22.3 ± .13	1.03 ± .09	4.62 ± .40
(K–2)	F_6	1910	20(?)	...	...	2	16	12	22	34	29	9	1	2	2	1	...	130	22.8 ± .11	1.82 ± .08	7.98 ± .33
(K–2)–1	F_7	1911	26	1	1	0	0	2	15	51	62	49	13	8	1	1	...	204	24.0 ± .07	1.45 ± .05	6.03 ± .20
(K–2)–1–6	F_8	1912	26	...	1	1	15	29	48	54	46	21	6	0	1	0	1	223	22.8 ± .07	1.63 ± .05	7.15 ± .23

TABLE XIII

Frequency Distribution of Number of Leaves in Family 73, Grown at Bloomfield, Conn.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant																Total	A.	S. D.	C. V.
				19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34				
(73–1)–2–1	F_9	1912	24	...	...	3	5	19	30	39	54	32	23	15	1	...	...	...	...	221	25.7 ± .08	1.83 ± .06	7.12 ± .23
(73–1)–2	F_8	1911	23	...	...	2	2	8	37	50	67	31	14	5	1	...	...	...	...	217	25.6 ± .07	1.46 ± .05	5.71 ± .19
(73–1)	F_7	1910	25	...	1	2	2	10	25	29	43	46	29	18	8	1	1	1	...	216	26.3 ± .09	2.01 ± .07	7.64 ± .25
73	F_6	1909	28	...	...	...	...	3	18	26	56	88	74	29	4	1	1	...	...	300	26.9 ± .06	1.45 ± .04	5.39 ± .15
(73–2)	F_7	1910	29	1	0	0	0	9	14	34	48	44	29	14	8	...	...	...	...	201	26.3 ± .08	1.73 ± .06	6.58 ± .22
(73–2)–3	F_8	1911	1	...	...	...	...	...	2	11	19	31	48	41	24	11	5	2	1	195	28.2 ± .09	1.80 ± .06	6.37 ± .22
(73–2)–3–3	F_9	1912	332	...	...	...	1	1	4	13	13	21	12	8	3	...	...	...	...	76	26.7 ± .13	1.65 ± .09	6.18 ± .34

the tobacco grower loses an average of from one to two of his most valuable leaves.

The plus strain of Family No. 56, which we were discussing when we digressed to speak of the critical periods of development, did show a considerable shifting of the mean following the selection of high-leaved mother plants. In the Bloomfield selections the mean went from 24.2 $\pm$ .06 to 26.7 $\pm$ .08 leaves, then to 26.8 $\pm$ .07 leaves; in the New Haven experiment the mean shifted to 27.4 $\pm$ .08 leaves,—a gain of 3.2 leaves,—and then dropped to 26.4 $\pm$ .11 leaves, recovering again in the F_9 generation to 27.5 $\pm$ .11 leaves; in the Forest Hills experiment the successive means were 27.2 $\pm$ .08, 28.9 $\pm$ .08 and 26.7 $\pm$ .06 leaves. Summing up the data from this experiment, it may be assumed to be reasonably certain that no progress resulted from the selection of minus extremes, but that there was a slight effect gradually diminishing in quantity when plus extremes were selected.

Representative plants of Family 56 obtained by three years of selection in the effort to produce strains of high and low leaf number, respectively, are shown in Figs. 8 and 9.

Family No. K (Table XII) was grown on a farm near the Bloomfield experiments, in 1910. The records of the F_5 generation consisted of the number of leaves of only 31 plants. From among these individuals two plants were selfed to become the mothers of the F_6 generation. Since no dependence can be placed on the F_5 distribution by reason of the few plants and since it is not absolutely certain that the mother plants of F_6 had 20 leaves each, the selection really began in 1911 with the F_7 generation. There is a difference between the minus strain and the plus strain in 1911 and 1912,—0.5 leaves the first year and 1.3 leaves the second year,—however, so that one may assume the possibility of a slow shifting of the mean in both directions.

The data on Family No. 73 are shown in Table XIII. This family came from a 28-leaved plant, one of the highest of the F_5 generation. The F_6 progeny of this

TABLE XIV

Frequency Distribution of Number of Leaves in Family 27, Grown at Bloomfield, Conn.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant													Total.	A.	S. D.	C. V.
				20	21	22	23	24	25	26	27	28	29	30	31	32				
(27–1)–1	F_7	1912	22	1	0	8	12	44	63	69	61	37	16	2	3	...	316	25.9 ± .07	1.75 ± .05	6.76 ± .18
(27–1)–1	F_7	1911	22	...	...	1	4	10	32	71	64	22	7	2	1	...	214	26.3 ± .06	1.32 ± .04	5.01 ± .16
(27–1)	F_6	1910	25	...	1	5	12	23	31	50	65	29	22	12	4	...	254	26.5 ± .08	1.94 ± .06	7.32 ± .22
27	F_5	1909	29	...	...	2	2	11	33	67	109	46	20	9	1	...	300	27.8 ± .06	1.40 ± .04	5.04 ± .14
(27–2)	F_6	1910	28	...	3	7	23	39	55	45	31	16	3	...	...	...	222	25.2 ± .07	1.63 ± .05	6.47 ± .21
(27–2)–1	F_7	1911	28	...	1	1	2	35	47	58	39	27	12	...	...	...	222	26.0 ± .07	1.50 ± .05	5.78 ± .19
(27–2)–1	F_7	1912	28	...	5	14	38	51	73	75	29	14	5	0	0	1	305	25.0 ± .06	1.67 ± .05	6.68 ± .18

TABLE XV

Frequency Distribution of Number of Leaves in Family 82, Grown at Bloomfield, Conn.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant													Total	A.	S. D.	C. V.
				20	21	22	23	24	25	26	27	28	29	30	31	32				
(82–2)–1	F_8	1912	30	...	1	5	6	13	21	48	60	43	20	3	3	2	225	26.7 ± .08	1.80 ± .06	6.74 ± .21
(82–2)–1	F_8	1911	30	...	...	...	2	11	35	53	62	37	12	4	1	...	217	26.6 ± .06	1.40 ± .05	5.27 ± .17
(82–2)	F_7	1910	28	1	0	2	4	21	31	41	36	30	22	13	3	...	204	26.6 ± .09	1.95 ± .07	7.33 ± .25
82	F_6	1909	30	...	...	...	7	15	38	73	91	60	16	1	1	...	297	26.6 ± .05	1.37 ± .04	5.08 ± .14

individual showed a mean of 26.9 ± .06 leaves, and from among them plants having 25 and 29 leaves, respectively, were selected to start the minus and the plus lines. These two mother plants gave F_7 populations alike as to mean, but differing by one class as to mode. The minus line had the higher mode. The extremes of this generation used in carrying on the experiment differed by 8 leaves, and the resulting progenies apparently followed the selection. The means are 25.6 ± .07 and 28.2 ± .09 leaves. Whether these shifted means represent a permanent change or not we are not prepared to say. The minus mean is probably somewhere near the correct figure for in the F_9 generation it was practically the same, but in the F_9 generation of the plus strain the mean dropped from 28.2 ± .09 leaves to 26.7 ± .13 leaves. This is a slightly lower point than that of the original F_5 distribution, but it was calculated from only 76 individuals. A conservative estimate of the significance of the results would probably be as follows: the mean of the minus strain has shifted slightly but permanently and is now fixed, while the mean of the plus strain has not changed but has shown evidence of some heterozygosis in one generation.

We come finally to consider Families No. 27 and No. 82, the data on which are listed in Tables XIV and XV. Two generations of both plus and minus selection were recorded for Family No. 27, but only plus selections of Family No. 82 were grown. There is no necessity for considering either in detail because a simple inspection of the tables shows that selection has accomplished nothing.

Conclusions

The cumbersome and no doubt dry details of the experiments to the close of the year 1912 having been described, let us give a brief résumé of the conclusions that we believe may reasonably be drawn from the data that have been offered. There can be no doubt that the original "Halladay" type of tobacco, isolated and propa-

gated by Mr. Shamel and Mr. Halladay from the cross between "Havana" and "Sumatra" tobaccos, arose through the segregation and recombination of the Mendelian factorial differences of the two plants, and not as a mutation. It is simply a union of the factors that stand for leaf size and height of plant in the "Havana" variety with the factors that bring about leaf shape and high number of leaves in the "Sumatra" variety. It happened that the somatic characters of these varieties account for all the characters of the hybrid. At the same time one must remember that strains were obtained by selection that averaged higher in number of leaves than did even the "Sumatra" parent. We can only conclude from this fact that the difference between the "Havana" and the "Sumatra" varieties in leaf number is greater factorially than somatically. Besides certain factors common to the two varieties, the factors for leaf number in "Havana" tobacco might be represented by the letters *AA,* and those of "Sumatra" tobacco by the letters *BB, CC, DD, EE.* By recombination, this would give plants with a smaller number of leaves than the "Havana" variety and plants with a greater number of leaves than the "Sumatra" variety. Both combinations were obtained; and further, the theory has been shown to be correct by the results of other crosses where both types appeared (Hayes, '12). It is probably unwise to suggest too concrete a factorial analysis of the cross, yet the factorial difference assumed above will account for all of the facts obtained, by simple recombination. We assume a factor in the heterozygous condition to account for the production of one leaf and a factor in the homozygous condition to account for the production of two leaves. The mean of the " Havana" variety is about 20 leaves and the mean of the "Sumatra" variety about 26 leaves. Somatically there is a difference of 6 leaves or three factorial pairs for which to account. But in order to have the theory coincide with the facts there must be at least one (possibly two or three) factorial difference that does not show in the two varieties. The meaning of this statement can

be shown best by an illustration. The 20 leaves of the "Havana" variety and the first 20 leaves of the "Sumatra" variety are represented by 10 pairs of factors, of which nine are the same and one different in the two strains. The "Havana" variety is nine leaf factors plus *AA*, the first 20 leaves of the "Sumatra" variety are nine leaf factors (the same as those in the "Havana") plus *BB*. The additional leaf factors of the "Sumatra" are *CC, DD. EE.* With these assumptions, the recombinations of a tetra-hybrid will represent our facts fairly accurately. But, as was stated above, it does not seem wise to take this interpretation of the facts too literally. That some such factorial combination will represent our facts superficially there can be no doubt, but in reality if one could grow hundreds of thousands of individuals and follow the behavior of each he would likely find himself constrained to represent his breeding facts by a much more complex system. There would probably be gametic couplings and factorial differences whose main effect would be on some entirely different character or complex of characters, but which would have some slight jurisdiction over leaf determination. To become diagrammatical, the unit characters of a house are its cornices, its windows, its floors and what not, but a collection of these components is not a house. We may even exchange dormer windows with our neighbor, but we can exchange them only if they fit. Again, we may put on a coat of paint, a color unit, but this color unit affects the appearance of many other parts that are just as truly units.

The essential part of our conception of the origin of this hybrid type is that recombinations of characters quantitative in their nature can be expected and predicted in crosses in exactly the same manner as is done with qualitative characters. On the other hand, it must be borne in mind that here was a hybrid type that appeared to be breeding true to the general characters that we have described, in the F_4 generation. That it was not breeding true is clear from the results of the selection experiments, yet out of the small number of F_5 and F_6 families

taken under observation at least two were found to be breeding true for all practical purposes in the F_5 and F_6 generations. We were able to reproduce the "Havana" type by continued selection in Family 77 and were able to produce strains breeding approximately true to 30 leaves or so by the selection of mother plants in several families. But can we say that any of our families are now fixed so that no progress can be made by selection? We can not. But we can say that some of them are so constant that it would be a loss of time for selection to be continued for economic results. It is important to know whether plant or animal populations can reach such a state of constancy by inbreeding that no profitable results can afterwards be obtained by the practical breeder. We believe it demonstrated by even these few data that such a state, a homozygous condition, occurs in a definite proportion of F_2 offspring, and can be propagated commercially at once if a sufficient number of families are grown to be relatively certain of including the desired combination.

As to the problem of theoretical importance, the question of the true constancy of homozygotes generation after generation, we believe it to be fair to conclude that a state so constant is reached, that even for the theoretical purposes of experimental genetics it may be assumed as actually constant. Further experiment and larger numbers may show that selection can always cause a shift in the mean, but will necessarily be a shift so slight that it can be detected only by a long-continued experiment and enormous numbers. Assuming for the purpose of argument that this is the case, the matter would affect only the question of the trend of evolution. It may come to be believed, from evidence now unknown, that evolution may progress slowly in this manner, but if it does, its course can hardly be demonstrated experimentally beyond a reasonable doubt. The problems of experimental genetics can be attacked, however, from the standpoint that experimental evidence of the shifting of the mean of a homozygous population by selection is negligible.

Mutations may occur. We have shown the origin of one family by a very wide mutation. In this particular case it was not difficult to show that a constitutional change took place in a single germ cell of the mother plant. It was only by a lucky chance that this fact could be demonstrated, for with smaller changes such proof would be impossible; but there is no reason to believe that this phenomenon is unique or even rare. It is much more reasonable to assume that mutations usually arise in single gametes than that the same change occurs simultaneously in many germ cells. One should expect the somatic result of a mutation in an hermaphroditic plant —the sporting plant itself—not to breed true, therefore, but to behave as an F_1 hybrid between a mutating and an unchanged germ cell. It is true that the mutations observed by DeVries in *Œnothera Lamarckiana* are supposed to have bred true, but this is sometimes questionable even from DeVries's own data. The Lamarckiana "mutants" that did breed true are much more reasonably explained as segregates from complex hybrids. They can be interpreted by Mendelism with no essential outstanding facts, but if they are to be interpreted as mutations, several discrepancies between what actually occurred and what should be expected on DeVries's own theory must be explained. It must be shown why the changes took place in numerous germ cells,—in both the male and the female gametes,—and why these germ cells always fused at fertilization; for the changed germ cells must have fused with each other because many *Lamarckiana* plants were produced by the same mother plants that produced the mutations, while the mutations are supposed to have bred true. On the only other possible theory of mutation, that the change occurred in the developing zygote after fertilization, one would have to explain why the mutants did not often appear as bud variations, instead of these being much rarer than the supposed mutations, as is actually the case.

We do not deny the theory of mutation as modified to

assume only that constitutional changes usually occur in the germ cells, but on this belief the sporting plants must often be F_1 hybrids, and the plant breeder must resort to selection to isolate his pure mutation. And by the same reasoning one gametic change may produce many new creations, for there is a chance to recombine it with all the known gametic differences in the species.

No one can say how often mutations arise. It is likely that changes other than the one observed took place in our tobacco experiments, but it is not likely that they are sufficiently numerous to base a system of selection within a pure race on the possibility of their occurrence. The fact that no changes ensued that could be detected in several of our selected lines is an argument against it. The comparatively large jumps are the ones likely to have the greatest economic importance, and these are easily detected without refined methods of procedure. Small jumps can be economically important only if they are numerous, and, as there are absolutely no data to show either that they are numerous or that changes can be produced rapidly within homozygous pure lines through any other cause, it seems unwise to recommend that the practical breeder expend time and money to bring about results that either can not be expected at all or that are so slow and so trifling that they can not be detected in carefully planned and accurately executed genetic investigations. On the other hand, the results of the last decade show that important economic results can be obtained easily and surely by selection from artificial hybrids or from the natural hybrids that occur in cross-fertilized species by the recombination of Mendelian factors. We believe, therefore, that the isolation of homozygous strains from mixtures that are either mechanical or physiological, that are either made artificially or are found in nature, offers the only method of procedure that the practical plant breeder will find financially profitable.

Finally, we should like to call attention again to the

practical importance of determining the duration of the period in the course of which particular plant characters are responsive to the action of environmental influences. The character complex that has been the basis of this study is a striking illustration of how results from such investigations may be applicable to farm practise. One may plant a portion of the seed from a self-pollinated tobacco plant on poor soil or on good soil and the average number of leaves per plant and the general variation of the plants in number of leaves will remain nearly the same in both cases.[2] But seed selected from *mother plants* grown on the good soil will produce plants averaging slightly higher in leaf number than the plants coming from seed on mother plants whose environment is poor. Consequently, it is better to select seed from well-developed mother plants—mother plants whose environment has been good—than from mediocre mother plants. There is no question here of the inheritance of an acquired character or of continuing to raise the number of leaves by cultural treatment. One simply takes advantage of the fact that during seed formation there is a period of mobility at which time the potential number of leaves of the young plant are practically fixed. Pending the end of this critical period, the number of leaves can be influenced by external conditions within the limit of fluctuating variability.

In the same connection, the effect of time of planting on the tobacco plant should again be mentioned, as this also emanates from environmental change. The actual number of leaves is, of course, practically fixed at the time of setting the plants in the field, but this is not true of the number of leaves that will have a commercial value. For example, a seedling with 26 potential leaves is planted. If it is planted when about four inches high, the general physiological disturbance due to transplantation is negligible and the plant continues its normal cycle of development without a pause, bringing to maturity

[2] Garner's (:12) results on Maryland Mammoth are an exception to this statement because this variety is indeterminate in growth.

about 22 leaves. If planting is delayed until the seedling is eight or ten inches high, there is a different state of affairs. Development is arrested, the plant pauses to adjust itself to the change. It soon recovers and continues its normal ontogeny, but the period of reduced growth has left an ineffaceable record. Several of the leaves—among them the more valuable leaves—have been so affected during this readjustment, that they develop to only a fraction the size that they should attain because the internodes between them are so short, due to the constricted development that normal metabolism does not occur. Thus there is a loss of one or two leaves, which on several acres of tobacco may make the difference between profit and loss. Hence, the grower should not delay setting his plants in the field until they have become overgrown in the seed bed.

March, 1913

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GYNANDROMORPHOUS ANTS DESCRIBED DURING THE DECADE 1903–1913

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In 1903 I described six gynandromorphous ants and reviewed the previously recorded cases, seventeen in number. Although many thousand ants have since passed through my hands, I have failed to find any additional cases. Other observers, however, have been more fortunate and have described seven within the past decade. As these are all very interesting, it seems advisable to give a brief account of them as a sequel to my former paper.

1. Lateral Gynandromorph of Cardiocondyla batesi Forel. var. nigra Forel.—Santschi (1903, p. 324, Fig. 5, *i*)

This specimen is female on the right and partly male on the left side. The male portions are sharply marked off from the black female portions by their testaceous red color. The line of demarcation, very clear in front, starts at the anterior clypeal border and divides the head into two nearly equal parts, but leaves the median ocellus on the male side. It then divides the pronotum down the middle and the three anterior quarters of the mesonotum. Thence the line fades out on the right side so that the whole posterior border of the mesonotum is male. Three quarters of the prescutellum and the anterior half of the scutellum are male. The epinotum and the abdomen are female throughout, but the female genitalia are slightly asymmetrical on the left side. The fore and middle legs on this side and a portion of the mesosternum are male. There are wings on both sides, but the anterior one on the female side was lost after capture. Those on the left

side are well-developed, with distinct venation and pale pterostigma, and are inserted in a distinctly male area. The specimen was not dissected.

Santschi found this ant in a nest with females at Kairouan, Tunis, but without males, either of the winged or of the ergatomorphic type, which is peculiar to this and some of the other species of *Cardiocondyla*. His attention was attracted by the bizarre movements of the specimen, as it turned around rather quickly in circles about 10 cm. in diameter, with the male portion inside. In other words, owing either to the asymmetry of its brain and visual organs or to differences in the length of the legs on the two sides of the body, it made circus movements like a normal insect which has had one of its eyes or optic ganglia injured.

2. Lateral Gynandromorph of Anergates atratulus Schenck.—Adlerz (1908, p. 3, Fig. 1, *a, b, c, d* and *f*)

An imperfect lateral gynandromorph, with the head largely male on the left, female on the right side, the light color of the male being sharply marked off from the dark color of the female only anteriorly. Thorax in front female, with wings equally developed on both sides (the male *Anergates* is wingless and pupoid!), but with pale (male) coloration on the left and dark (female) coloration on the right side, the line of division between the two neither sharp nor straight and the whole postscutellum blackish brown. Abdomen with irregular arrangement of color. Petiole black on the right, grayish yellow on the left; postpetiole mostly blackish brown, but with a large grayish yellow spot on the left side of its anterior surface. Third dorsal tergite blackish brown on the right, grayish yellow on the left side. Remainder of gaster grayish yellow, tinged here and there with pale brown. Third tergite with a median longitudinal groove which runs back on to the succeeding segment as in the virgin female. The left side of the abdomen has seven complete segments and well-developed genitalia; the right

side has only six complete segments and a membranous, incomplete seventh. The genitalia on the right side are imperfect, the volsella being represented only by a piece corresponding to its dorsal portion and the stipes is completely lacking. The legs are of the female type, except the left fore leg, which is male, although the tibial spur (strigil) is pectinate as in the female. This spur is known to be nonpectinate in male Swedish, but pectinate in male Swiss *Anergates* specimens.

On dissecting this specimen, which he took from a large *Anergates-Tetramorium* colony near Arkösund in Östergötland, Sweden, Adlerz found on the left side a well-developed vesicula seminalis, receiving a vas deferens half as long. No traces of female reproductive organs nor of the poison gland and vesicle could be detected.

Of particular interest was the behavior of this gynandromorph, because, as Adlerz says, it evidently felt itself to be a male but was treated by the normal males in the colony as a female. Its movements were somewhat livelier than those of normal males, and it at first made feeble attempts to copulate with the females and was treated with indifference by the males. A few days later it became more energetic and persistently attempted to copulate, especially with one particular female, although always unsuccessfully while it was under observation. It was evidently inflamed with the insatiable sexual appetite so characteristic of the normal *Anergates* males, which, being wingless, always mate with their sisters before they fly out of the parental nest. On the following day, however, a normal male made the most persistent efforts for several hours to mate with this same gynandromorphous individual. Adlerz concludes that

this indicates that the males regarded it as a female. Of course, we may suppose that its wings made it seem like a female and attracted the male, but from the fact that males attempt to mate even with female pupae and therefore with a stage which has not yet developed wings, it is more probable that the male was attracted to the gynandromorph by some female odor. At any rate the double nature of the gynandromorph

is even more strongly indicated by the facts just recorded than by its morphological peculiarities.

3. LATERAL GYNANDROMORPH OF ANERGATES ATRATULUS SCHENCK.—ADLERZ (1908, p. 5, Fig. 2, *a, b, c, d* and *e*)

An imperfect lateral gynandromorph, male on the left, female on the right side, resembling the preceding specimen, but with the dark female color more pronounced on the male side of the head. There were well-developed wings on both sides of the thorax, which was of the female form though dark on the right and pale on the left side, except the epinotum, which was grayish yellow throughout. Abdomen in color and form almost typically male, with the genitalia well-developed on both sides, but with a feeble mid-dorsal impression recalling the condition in the virgin female. Legs of the female type, except the left fore one, which is somewhat shorter and thicker as in the male and with the tibial spur (strigil) cleft but not pectinated.

Dissection showed the reproductive organs to be in the same condition as in the preceding specimen; *i. e.*, they were present only on the left side and consisted of a rather large vesicula seminalis with its vas deferens. No traces of female reproductive organs, nor of a sting or poison apparatus were to be found.

This specimen was taken from the same nest as the preceding.

4. LATERAL GYNANDROMORPH (ERGATANDROMORPH) OF FORMICA SANGUINEA LATREILLE.—DONISTHORPE (1909, p. 464, Fig. 1)

A nearly complete lateral ergatandromorph, with the right antenna, mandible and eye, and right and median ocellus male and the left antenna, mandible, eye and ocellus of the worker type. Head black, except the left mandible, left half of clypeus, left cheek and a small patch in front of the eye, which are red. Thorax and petiole

male on the right, worker on the left, the line of division running to the left of the median line so that the black of the right side of the mesonotum encroaches on the red color of the left side. Petiole and gaster sharply divided into black right and red left halves, the right half of the latter also with male pilosity and sculpture. External male genitalia and anal sternite on the right side. The red and black coloration is sharply divided on the venter, but the coxæ are all black and red as on the male, and the legs on both sides are somewhat infuscated. Tarsi longer on the right (male) side. Wings well developed, on the right side only, with pale veins and stigma and more like those of the female. Length 7 mm.

This specimen was taken by Mr. Donisthrope July 20 or 21 from a large colony in Bewdley Forest, England.

5. Lateral Gynandromorph of Formica sanguinea Latreille.—Donisthorpe (1909, p. 464, Fig. 2)

A nearly complete lateral gynandromorph, male on the left, female on the right side. The head is of the female type, rather small, with both of the antennæ and the ocelli female and the left eye a little larger than the right. Head black, clypeus and right mandible red; thorax evenly divided into a black left and red right half, but only the upper right corner of the epinotum red. A piece of the scutellum and postscutellum red on the left side where the wing is inserted. Petiole sharply divided into a red right and left black half. Gaster black, the pilosity and sculpture on the right half female, on the left half male, the color being sharply defined on the venter. Legs and coxæ female on the right, male on the left side. External genitalia of the male type present on the left side. Both pairs of wings fully developed, but the stigma and veins darker as in the male. Length 9 mm.

This specimen was taken from the same colony as the preceding.

6. Frontal Gynandromorph of Solenopsis fugax Latreille.—Santschi (1910, p. 649)

The head and thorax in this specimen are female, the pedicel and gaster male. The head is somewhat smaller than in normal females. The copulatory organs are those of the normal male. Santschi remarks that it "would be interesting to observe the sexual behavior of such an individual possessing a female brain and male genitalia."

7. Lateral Gynandromorph (Ergatandromorph) of Myrmica scabrinodis Nylander.—Donisthorpe (1913, p. 44, Pl. I)

A nearly complete lateral ergatandromorph; worker on the right, male on the left side, the former being blackish, the latter reddish yellow. Right half of head larger than the left, but with a smaller eye, striatorugose; right antenna yellow, with a three-jointed club, its scape with the usual strong lateral tooth at the basal flexure. Right half of thorax yellow, its epinotal half with a strong spine; right half of petiole and postpetiole yellow, rugose and punctured; right half of gaster pale fuscous yellow. Legs on the right side of the worker type, yellow. Left side of head blackish, punctate, not striatorugose, with a larger eye and the median and left ocellus; its antenna fuscous, with four-jointed club. Left half of thorax blackish, its epinotal portion unarmed; left half of petiole and postpetiole smooth, fuscous black. The greater part of the left half of the gaster had been eaten away but the remainder was darker fuscous than the right. Legs on left side of the male type, fuscous; wings on the left side only.

Donisthorpe remarks that this specimen, which was picked up dead by Mr. Dollman at Ditchling, England, approaches the var. *sabuleti* Meinert in having the left antennal scape longer than in the typical male *scabrinodis* and the tooth on the right antenna large.

In conclusion I would call attention to a peculiar ant described by Mayr (1868, p. 60) from the Baltic amber

and designated as a "Zwitter" (gynandromorph) of *Hypoclinea constricta* Mayr, or *Iridomyrmex constrictus* as we must now call the species. Through the kindness of Prof. A. Tornquist, of the University of Königsberg, I have been able to examine this specimen in connection with many other amber Formicidæ. The general structure of the head, thorax and gaster is that of a worker, though the thorax is not typical, as the base of the epinotum is less convex and less abruptly elevated, so that the angle between it and the declivity is less pronounced in profile. Mayr does not mention that the eyes are decidedly larger and more convex than in the normal worker and therefore more like those of the male. There are a few small white spots or bubbles on the vertex, which resemble small ocelli, but these organs seem to be actually absent. The antennæ are 13-jointed and very long, as in the male; the scapes, however, are like those of the worker, but extend well beyond the posterior borders of the head, whereas joints 2–11 of the funiculi are cylindrical, subequal and fully three times as long as broad, the terminal joint being somewhat longer than these, the first shorter. In the gaster, which is shaped as in the normal worker, there are five distinctly visible segments, but the tip shows clearly the small, hairy, external genital valves (stipes) of the male. The legs are also more slender than in the normal worker and therefore more like those of the male.

At first sight this singular insect seems to be a gynandromorph, as Mayr supposed, or more specifically, an ergatandromorph of the blended type, with worker characters preponderating in the trunk and those of the male preponderating in the eyes, appendages and genitalia. It is possible, however, to regard this specimen as an ergatomorphic male, like those which occur normally in certain species of *Ponera, Cardiocondyla, Formicoxenus, Symmyrmica* and *Technomyrmex*. Unfortunately we are not in a position to decide between these alternatives, because we are dealing with a single fossil specimen and are not even sure that it belongs to the species to which Mayr

assigned it. Still the case is interesting if only because it suggests the further question as to whether the ergatomorphic males in the genera above cited may be regarded as originally frontal ergatandromorphs, with worker head and thorax and male gaster, that have become the only males of the species. If this is true, the ergatomorphic males may have arisen by mutation from pathological or teratological forms and have been preserved in certain species in which peculiarities of habit rendered the fecundation of the virgin females in the nest by wingless males more advantageous than the type of mating exhibited by the nuptial flight. A moment's reflection shows that the nuptial flight is a highly advantageous institution in common ants that form large colonies, but must be as decidedly disadvantageous in the case of very small, rare ants whose colonies are very sporadic and comprise only a few individuals. This is actually the condition seen in all the species with ergatomorphic males in the genera *Ponera*, *Cardiocondyla*, *Formicoxenus*, *Symmyrmica* and *Technomyrmex*, and may be supposed, therefore, to account for the substitution of the wingless, ergatomorphic for the normal winged males in these species.

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SHORTER ARTICLES AND DISCUSSION

ON THE RESULTS OF INBREEDING A MENDELIAN POPULATION: A CORRECTION AND EXTENSION OF PREVIOUS CONCLUSIONS[1]

In a recent paper by the present writer on inbreeding,[2] the conclusion was reached (*loc. cit.*, p. 608)

> that no increase in the proportion of homozygotes in the population follows inbreeding save under one or the other of two special conditions, viz.:
>
> (*a*) Continued self-fertilization.
>
> (*b*) Some form of gametic assortative mating which increases the natural probability of like gametes uniting to form zygotes.

This conclusion is entirely correct as it stands, but also barren, for it overlooks the very essential fact that any sort of inbreeding involves in greater or less degree "gametic assortative mating." The mathematical demonstration on page 608 of the paper referred to is also entirely correct so far as it goes, but it stops too soon. Up to the third generation of brother × sister mating starting from a population of complete heterozygotes there is no increase in the proportion of homozygotes beyond that prevailing in a general Mendelian population. In the fourth and later generations there is, however. The blunder, kindly pointed out to me by Professor E. M. East, which in retrospect seems altogether too stupid even to be possible, was in the failure to recognize that after the second generation the constitution of the *family* would no longer be the same as that of the population. This is the point which makes illegitimate the extension by induction of the results up *to* the third generation to the generations beyond.

The general conclusion of the former paper quoted above, should then be as follows: An increase in the proportion of homozygotes in the population will follow inbreeding of any sort, though at different rates for different types of inbreeding, *because any inbreeding involves homogamy (or assortative mating) in some degree.*

Having made clear the location and nature of the error I desire now to show in some detail exactly what results follow from con-

[1] Papers from the Biological Laboratory of the Maine Agricultural Experiment Station, No. 54.

[2] "A Contribution Towards an Analysis of the Problem of Inbreeding," American Naturalist, Vol. XLVII, pp. 577–614, 1913.

tinued brother × sister mating in a Mendelian population. To this we may now proceed.

The Distribution of a Mendelian Population in Successive Generations with Continued Brother × Sister Mating

Let us start with a population composed entirely of complete heterozygotes. We shall consider a single character pair, A denoting the dominant character, and a the recessive. The complete heterozygote individual will then be Aa, and will produce in equal numbers A and a gametes.

In making an analysis of the effect of inbreeding on the population it will be necessary to deal not merely with the distribution of individuals in each generation, but also with the distribution of families of the several types. Each mating will produce an array of families, as well as an array of individuals. The standard family throughout this discussion is taken as including 32 individuals, of which 16 are males and 16 females. It is further assumed that there is no sex-linkage of characters, and that in any family there will be an equal number of brothers and sisters of each zygotic constitution represented. One family of 16 pairs of brothers and sisters will make 16 matings and produce 16 families of 32 individuals each. This constant rate of fertility is assumed throughout the discussion.

Every mating made is of a brother with his sister.

With so much by way of preliminary definition of the limitations of this investigation, let us proceed to the actual analysis.

First Generation

Constitution of the Population.—By hypothesis all individuals are Aa.

Proportion of Homozygotes in this Generation.—0 per cent. of the whole population.

Matings to Produce the Second Generation.—Start with one brother × sister pair of individuals from this population. The mating will be $Aa \times Aa$. This will produce *one family*, $8AA + 8Aa + 8aA + 8aa$.

Second Generation

Constitution of the Population.—$8AA + 8Aa + 8Aa + 8aa$.

Proportion of Homozygotes in this Generation.—50 per cent. of the whole population.

Matings to Produce the Third Generation.—The matings of the one family of this generation will be as follows:

♂♂	♀♀	♂♂	♀♀
(1) *AA*	(1) *AA*	(9) *aA*	(3) *aA*
(2) *AA*	(5) *AA*	(10) *aA*	(7) *aA*
(3) *AA*	(9) *AA*	(11) *aA*	(11) *aA*
(4) *AA*	(13) *AA*	(12) *aA*	(15) *aA*
(5) *Aa*	(2) *Aa*	(13) *aa*	(4) *aa*
(6) *Aa*	(6) *Aa*	(14) *aa*	(8) *aa*
(7) *Aa*	(10) *Aa*	(15) *aa*	(12) *aa*
(8) *Aa*	(14) *Aa*	(16) *aa*	(16) *aa*

Third Generation Families Produced.—(Note: the numbers in parenthesis are to identify matings and their consequent families.)

	AA	*Aa*	*aA*	*aa*
(1)	32	....	....	....
(2)	16	16	....	....
(3)	16	16	....	....
(4)	....	32	....	....
(5)	16	....	16	....
(6)	8	8	8	8
(7)	8	8	8	8
(8)	....	16	....	16
(9)	16	....	16	....
(10)	8	8	8	8
(11)	8	8	8	8
(12)	....	16	....	16
(13)	....	....	32	....
(14)	....	....	16	16
(15)	....	....	16	16
(16)	....	....	....	32

Third Generation

Constitution of the Population.—

$$128AA + 128Aa + 128aA + 128aa.$$

Proportion of Homozygotes in this Generation.—50 per cent. of the whole population.

Fourth Generation Families Produced.—The third generation families, when mated, will produce families as follows:

Summarized this gives the following fourth generation *families* produced:

$(1)_4$ 36 families like $(1)_3$
$(2)_4$ 24 families like $(2)_3$

$(3)_4$ 4 families like $(4)_3$
$(4)_4$ 24 families like $(5)_3$
$(5)_4$ 80 families like $(6)_3$
$(6)_4$ 24 families like $(8)_3$
$(7)_4$ 4 families like $(13)_3$
$(8)_4$ 24 families like $(14)_3$
$(9)_4$ 36 families like $(16)_3$

	AA	*Aa*	*Aa*	*aa*
Family $(1)_3$ will produce . . 16 families of constitution	32	......	......	......
Families $(2)_3$ will produce 4 families of constitution	32	......	......	......
$(3)_3$, $(5)_3$ will produce.... +4 families of constitution	16	16	......	......
and $(9)_3$ will produce.... +4 families of constitution	16	......	16	......
each will produce....... +4 families of constitution	8	8	8	8
Families $(4)_3$ will produce 16 families of constitution	8	8	8	8
and $(13)_3$	......	......	......	......
each	......	......	......	......
Families $(6)_3$ will produce. 1 family of constitution	32	......	......	......
$(7)_3$, $(10)_3$ will produce... +2 families of constitution	16	16	......	......
and $(11)_3$ will produce... +1 family of constitution	......	32	......	......
+2 families of constitution	16	......	16	......
+4 families of constitution	8	8	8	8
+2 families of constitution	......	16	......	16
+1 family of constitution	......	......	32	......
+2 families of constitution	......	......	16	16
+1 family of constitution	......	......	......	32
Families $(8)_3$ will produce 4 families of constitution	8	8	8	8
$(12)_3$, $(14)_3$ will produce.. +4 families of constitution	......	16	......	16
and $(15)_3$ will produce... +4 families of constitution	......	......	16	16
each will produce....... +4 families of constitution	......	......	......	32
Family $(16)_3$ will produce 16 families of constitution	......	......	......	32

Fourth Generation

Constitution of the Population.—

$$2560AA + 1536Aa + 1536aA + 2560aa.$$

Proportion of Homozygotes in this Generation.—62.5 per cent. of the whole population.

Fifth Generation Families Produced.—The third generation families, when mated, will produce families as follows:

$(1)_4$ will produce $36 \times 16 = 576$ families like $(1)_3$
$(2)_4$ will produce $24 \times 4 = 96$ families like $(1)_3$
$+ 96$ families like $(2)_3$
$+ 96$ families like $(5)_3$
$+ 96$ families like $(6)_3$
$(3)_4$ will produce $4 \times 16 = 64$ families like $(6)_3$
$(4)_4$ will produce $24 \times 4 = 96$ families like $(1)_3$
$+ 96$ families like $(2)_3$
$+ 96$ families like $(5)_3$
$+ 96$ families like $(6)_3$

$(5)_4$ will produce	80	families like $(1)_3$
	$+ 80 \times 2 = 160$	families like $(2)_3$
	$+ 80$	families like $(4)_3$
	$+ 160$	families like $(5)_3$
	$+ 80 \times 4 = 320$	families like $(6)_3$
	$+ 160$	families like $(8)_3$
	$+ 80$	families like $(13)_3$
	$+ 160$	families like $(14)_3$
	$+ 80$	families like $(16)_3$
$(6)_4$ will produce	$24 \times 4 = 96$	families like $(6)_3$
	$+ 96$	families like $(8)_3$
	$+ 96$	families like $(14)_3$
	$+ 96$	families like $(16)_3$
$(7)_4$ will produce	$4 \times 16 = 64$	families like $(6)_3$
$(8)_4$ will produce	$24 \times 4 = 96$	families like $(6)_3$
	$+ 96$	families like $(8)_3$
	$+ 96$	families like $(14)_3$
	$+ 96$	families like $(16)_3$
$(9)_4$ will produce	$36 \times 16 = 576$	families like $(16)_3$

Summarized this gives the following fifth generation families produced:

$(1)_5$	848	families like $(1)_3$
$(2)_5$	352	families like $(2)_3$
$(3)_5$	80	families like $(4)_3$
$(4)_5$	352	families like $(5)_3$
$(5)_5$	832	families like $(6)_3$
$(6)_5$	352	families like $(8)_3$
$(7)_5$	80	families like $(13)_3$
$(8)_5$	352	families like $(14)_3$
$(9)_5$	848	families like $(16)_3$
	4096 $(= 16 \times 256)$.	

Fifth Generation

Constitution of the Population.—

$$44{,}736AA + 20{,}480Aa + 20{,}480aA + 44{,}736aa.$$

Proportion of Homozygotes in This Generation.—68.75 per cent. of the whole population.

Sixth generation families produced:

17,216	families like $(1)_3$
4,480	families like $(2)_3$
832	families like $(4)_3$
4,480	families like $(5)_3$
11,520	families like $(6)_3$
4,480	families like $(8)_3$
832	families like $(13)_3$
4,480	families like $(14)_3$

17,216 families like $(16)_3$

65,536 (= 16 × 4,096).

Sixth Generation

Constitution of the Population.—

$$786{,}432AA + 262{,}144Aa + 262{,}144aA + 786{,}432aa.$$

Proportion of Homozygotes in This Generation.—75 per cent. of the whole population.

From this point on it will not be necessary to carry out the work in detail. The final results are given in Table I for four more generations.

TABLE I

SHOWING THE CONSTITUTION OF THE POPULATION AFTER 7 TO 10 GENERATIONS OF BROTHER × SISTER MATING

Generation	*AA*	*Aa*	*aA*	*aa*	Percentage of Homozygotes in Whole Population
7	13,369,344	3,407,872	3,407,872	13,369,344	79.69
8	224,395,264	44,040,192	44,040,192	224,395,264	83.59
9	3,724,541,952	570,425,344	570,425,344	3,724,541,952	86.72
10	61,337,501,696	7,381,975,040	7,381,975,040	61,337,501,696	89.26

It is evident that the proportion of homozygotes is approaching 100 per cent. in the same manner as in the case of self-fertilization, worked out by East, Jennings and others, but at a slower rate.

In a later paper I hope to take up the problem of the general formulæ for finding the constitution of a Mendelian population after *n* generations of inbreeding of the different types, and at the same time discuss the relation of these results to the coefficients of inbreeding described in my former paper. It should be specifically mentioned that, in the light of the data here set forth, those criticisms of the conclusions of East and Hayes made in my former paper[3] which were based on the erroneous assumption of a fundamental difference between self-fertilization and all other forms of inbreeding in respect to homozygosis, have no validity whatever. It scarcely needs to be said that the blunder on the theoretical side here corrected in no wise affects the usefulness of inbreeding coefficients.

RAYMOND PEARL

[3] Cf. Pearl, *loc. cit.*, p. 606, 609 and 610.

ISOLATION AND SELECTION ALLIED IN PRINCIPLE

There are those who fully recognize the influence of natural selection in transforming the hereditary characters of a species, but are unable to see how isolation should have any effect of that kind. They say that you may divide a species into two branches between which all possibility of crossing is completely prevented, but if the environment surrounding each branch is the same, the natural selection to which each is subjected will be the same, and no divergence of character will take place. They forget that the separate branches, if prevented from crossing for many generations, are sure to develop different types of variation, and in due time different methods of using the same environment, and are therefore liable to subject themselves to different forms of selection. Again they forget that when the power of dispersal is highly developed in a species it may be exposed to diverse environments and therefore to diversity of selecting influences, and still remain one harmonious species, because free crossing is maintained between all parts of the species. As long as there is no isolation of different branches, that is, while free crossing continues, there is no permanent divergence resulting in diverse races or species, even though the one species is exposed to different forms of selection in different parts of its habitat.

Diversity of evolution, producing many divergent forms of animals, could never have arisen without continuous isolation between the different forms.

Again there are those who maintain that selection unaided by isolation can not produce transformation. It is true that divergent groups can not be produced and intensified without isolation; but a given race may be transformed by selection without being divided into two groups by isolation.

Heredity with variation is the active cause of transformation; isolation and selection are the conditions that shape the forms of heredity and variation.

It is a law of heredity, that, if those of a given stock that are most alike in hereditary characters mate with each other, there will be a tendency in their offspring to a stronger emphasis of that character.

Another law of heredity is that as long as free crossing is maintained between the different forms of a species these forms can not become widely divergent. The elephant and the mouse could never have been developed from one original stock while free crossing continued.

Now there are many ways by which the free crossing of one variation with others of the same species may be prevented, but they all come under two groups.

Under selection are classed all the influences enabling certain variations to reproduce more successfully than other variations, and so preventing free crossing between the successful and the unsucessful. Under isolation are classed all the influences that prevent living, and sexually reproducing creatures, from freely crossing.

Under normal conditions there is no crossing between the ass and the horse, though there is reason to believe that the early ancestors of each were of one stock freely interbreeding and producing fertile offspring. If isolation had not existed for ages between them, they could not have become the separate creatures that they now are. Heredity can combine only compatible characters. In some cases, incompatible characters arise between creatures of the same race preventing any crossing between them, as when a dextrally twisted mollusk produces a sinistrally twisted one; but, in most cases, such incompatibility arises only after isolation, through geographical separation, for many generations.

In view of these facts, is it not plain, that, in the case of a variable and plastic organism, races more or less divergent will be produced, if for many generations the organism is divided into branches that are prevented from crossing? Is not such a result just as sure as the gradual transformation of the race under a slow change of climate, when the successful variations are prevented from crossing with the unsuccessful variations?

JOHN T. GULICK

HONOLULU, T. H.

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SOME NEW VARIETIES OF RATS AND GUINEA-PIGS AND THEIR RELATION TO PROBLEMS OF COLOR INHERITANCE

PROFESSOR W. E. CASTLE

HARVARD UNIVERSITY

The marvelous color variation of the domesticated animals has been recognized as a capital illustration of evolution from the time of Darwin to the present, and much study has been devoted to the question of how it has taken place. Nevertheless we have very little positive information as to how existing color varieties originated, and theories differ concerning the matter.

It becomes therefore important to record carefully any contemporary events which may throw light on the subject. This is my excuse for calling the attention of scientists to the recent appearance in England of two new and striking color variations of the common or Norway rat. I say "appearance" advisedly for it is impossible to say how long these variations may have been in existence within the race, cropping out perhaps from time to time sporadically. Certain it is, however, that they have only quite recently come to the attention of "fanciers," who have taken them up with great enthusiasm.

The new varieties are known to the fancy as (1) *pink-eyed* yellow, fawn, or cream; and (2) *black-eyed* yellow, fawn, or cream. From the evidence at hand it is clear that each of the two variations has originated *in the wild*

race and *as a mutation* or unit-character variation, *retrogressive* in nature (*i. e.*, due to loss of some normal constituent from the germplasm). Each is a simple Mendelian recessive character in crosses with wild race, and with certain at least of the tame varieties. The two variations have not as yet been combined by intercrossing, but this will be attempted soon and, I doubt not, with entire success.

My first information about the new variations was obtained from *Fur and Feather,* the official organ of the English fanciers, in which appeared advertisements of "the new variety" of black-eyed yellow rat. Now as long ago as 1903 Bateson had commented on the singular absence of a "yellow" variety among rats, noteworthy because nearly all mammals kept in captivity have such varieties; and I have since been bold enough to publish some speculations as to why this variation had not made its appearance. Consequently I was much excited to learn that it actually had appeared. Miss M. Douglas, one of the editors of *Fur and Feather,* and secretary of the National Mouse and Rat Club (of England) very kindly answered my inquiries about the new varieties and put me in communication with the "originators," who have given so clear and full accounts of their procedure in establishing the new varieties that even the genetic behavior of the variations is fairly certain, though I purpose to confirm this fully with experiments which are already in progress.

The pink-eyed variation made its appearance first, so far as known, about 1910 or 1911, but it had probably been in existence for some time and become rather widely diffused throughout the central part of England, for at about the same time pink-eyed wild rats were caught at or near Preston and at Chesterfield, cities some 65 miles apart. I am informed that Mr. T. Robinson at Preston and Mr. W. E. Marriott at Chesterfield independently established the "pink-eyed fawn" variety, or what would better be called the *pink-eyed agouti* variety, since appar-

ently it differs from the wild gray (or agouti) variety by the pink-eyed variation alone. It is not a true *yellow* variety at all genetically, though (like the pink-eyed gray mouse) it resembles one superficially because of the yellow ticking of the agouti fur.

It is also quite distinct genetically from the *albino* variation seen in white rats, yet its "dirty white" color is enough like the appearance of the albino to permit mistaking one for the other. Possibly this is why the pink-eyed variation may have been for some time overlooked.

Mr. Robinson has not answered my inquiries, but Mr. Mariott writes in detail about his observations and experiments.

Under date of October 11, 1913, he says:

> The first rat with any semblance of fawn in it that I had was caught in a trap on a provision merchant's premises in Chesterfield. You could scarcely call it a fawn, but more of a cream or dirty white. I have also had four others similar to this one, 2 caught at the same place and 2 caught at a malt-house in close proximity to the other premises, [in all] 3 bucks and 2 does, but the only one that I was able to get to breed was the first brought to me, which was a buck. When first caught it was very wild, in fact it appeared to me to be more wild than an ordinary wild rat. It was a source of trouble getting it to mate, killing no less than 20 does before mating. I eventually got it mated to 2 does, one a pure white for at least 10 generations, and one black-and-white hooded-and-striped, or Japanese rat. The result of the pure white cross was 2 young, a buck and a doe, *which were agoutis with no white at all.*[1] The result from the Japanese cross was 7 young, 5 does and 2 bucks, which were the color of Irish agoutis being agouti color with a white stripe running underneath. These results naturally caused me great disappointment as I was expecting a fawn colored young one. When the young were old enough I mated father and daughter, result *nil;* mother and son, result *nil;* brother and sister. The brother and sister mating from the pure white cross produced 2 fawn colored rats, a buck and a doe, and 5 agoutis.[2] The brother and sister mating from the Japanese cross produced 2 fawn-and-white Japanese, 1 cream-and-white Japanese,

[1] Italics mine. Note the reversion to full wild color. This shows the pink-eyed variation to be entirely different in nature from the ordinary albino variation.

[2] Note the return of "fawn" (pink-eyed agouti) as a recessive character in approximately 1 in 4 young.

1 black-and-white Japanese, and 4 agoutis.[3] The fawns and fawn-and-whites resulting from these crosses were much deeper in color than the wild grandsire. Mated one with another they gave a proportion of about 2 fawn colored or fawn-and-white in 7 young.[4] I may say in conclusion that the original wild rat was in shape of body, skull, etc., as the ordinary brown or agouti rat that we have running wild in this district.

Mr. Marriott sold a "fawn-and-white" (pink-eyed hooded agouti) buck to Mr. E. F. Tilling, of Hessenford, who also "originated" the second variation, the "black-eyed yellow," or true yellow variation. His results from the pink-eyed variation confirm those of Mr. Marriott.

Mr. Tilling writes under date of October 18, 1913:

I see by *Fur and Feather* this week that you are interested in the yellow and cream varieties of rats. I am also much interested in these and have produced the latter variety within the last few months. We have 2 kinds over here, the yellow-and-white hooded with pink eyes and the self yellow (and cream) with black eyes. Both are quite distinct. The first mentioned was produced some 2 or 3 years ago. Mr. Marriott, of Chesterfield, bred the first I heard of from a wild caught fawn. He bred a couple of yellow and white hooded bucks of which Miss Douglas bought one and I the other. I mated mine to about 15 does of various colors and definite strains. He was a splendid breeder and got some very fine youngsters, but *not one of his own color from the first cross.*[5] I subsequently mated him to some of his daughters and they produced a good proportion of yellow-and-white young.[6] These are now fairly plentiful over here and are in the hands of several fanciers.

Of the other kinds, black-eyed fawns and creams, the first one exhibited and from which all mine are descended, was a very fine wild caught, deep colored, fawn specimen. I got her partly tame and exhibited her at the National Mouse and Rat Club's annual show at Bristol on November 27 and 28, 1912, where she won first in the self class and

[3] "Fawn- and white Japanese" means (to me) pink-eyed agouti with the "Japanese" color pattern (hooded). The formation of this class of young shows the hooded pattern ("Japanese") to be independent in transmission of the pink-eyed variation. "Cream-and-white Japanese," I interpret as pink-eyed *black* (non-agouti) hooded. "Black-and-white Japanese" is the familiar black hooded. We should expect this mating to produce also *self* pink-eyed agouti and *self* pink-eyed black which are not mentioned.

[4] The Mendelian expectation is 2 in 8.

[5] Italics mine. Note again the recessive nature of the variation.

[6] Not real yellow-and-white, as already explained, but pink-eyed agouti-and-white or black-and-white.

was well commented upon in the fanciers' papers. From this doe I have built up my strain of black-eyed creams. I mated her to a self black buck and she bred 8 youngsters all wild colored.[7] This is the only litter I had from her, as shortly afterward, during my illness, my man while transferring her from one cage to another let her get away and was unable to recapture her. However, I have bred from her youngsters, mating brother and sister, and the litters have invariably contained at least 1 fawn or cream[8] each time. I have now just bred for the first time from the 3 first does so produced, again mating them to their brother and the result is litters of 7, 5 and 7, respectively, all self creams.[9]

From the statements of Messrs. Marriott and Tilling, it is evident that the two variations, which they, respectively, have introduced into the rat fancy, are both recessive in heredity, as are also the three previously known Mendelizing color variations of rats, viz., (1) the albino variation (with uncolored coat and eyes); (2) the black variation (lacking the agouti ticking of the fur); and (3) the piebald "hooded" pattern of white and colored fur. Each of these is known to be an independent Mendelizing unit-character. If the new variations are as supposed independent of each other and of those previously known, they will make possible the immediate four-fold increase in number of the previously known color varieties of rats. If for the present we adopt a simplified terminology (as I have elsewhere suggested) for the different color variations, employing small letters for such as are recessive in heredity, we may use the following set of symbols:

White (albino)	$= w$,
Black	$= b$,
Hooded	$= h$,
Pink-eyed	$= p$,
Yellow	$= y$.

[7] This shows that the original yellow animal was potentially an *agouti*. A pair of yellows which Mr. Tilling has sent me have *light bellies* and I presume are also potentially agoutis.

[8] "Cream" here probably means yellow not transmitting agouti. It probably lacks the lighter belly as do yellow rabbits which do not transmit agouti.

[9] This shows that extracted yellows breed true to yellow. Hence the variation is recessive, as in rabbits and guinea-pigs, not dominant as in mice.

By various combinations of these variations, if each is independent of all the others, 32 varieties become possible. Half of these varieties will be albinos, white and so visibly indistinguishable. The other 16, we have reason to suppose, will look different from each other. Previously we had but four of these, the first four in the following list of the theoretically possible 16.

1. *Normal or wild* ...... *agouti.*
2. *b* .... *black,*
3. *h* .... *hooded,*
4. *bh* .... *black hooded,*
5. *p* .... pink-eyed,
6. *pb* .... pink-eyed black,
7. *ph* .... pink-eyed hooded,
8. *pbh* .... pink-eyed black hooded,
9. *y* .... yellow,
10. *yb* .... yellow black (*i. e.*, non agouti yellow),
11. *yh* .... yellow hooded,
12. *yp* .... yellow pink-eyed,
13. *ybh* .... yellow black hooded,
14. *ypb* .... yellow pink-eyed black,
15. *yph* .... yellow pink-eyed hooded,
16. *ypbh* .... yellow pink-eyed black hooded.

Varieties 1–4 have been known for some time; they have constituted the fancier's entire repertoire up to the present time. Varieties 5 and 9 have apparently arisen as wild sports obtained by Marriott and Tilling, respectively. By crosses these gentlemen have apparently obtained varieties 6, 7, 8, and probably 10. Varieties 11–16 are as yet unknown, but will doubtless soon be produced. Corresponding with each of the 16 colored varieties, an uncolored one should be possible of production, which would transmit in crosses with any colored variety the characteristics indicated by its formula. Albinos corresponding to colored varieties 1–4 are positively known to occur; their symbols would be *w*, *wb*, *wh* and *wbh*, respectively. Symbols for the remaining 12 expected varieties may be formed in like fashion, by prefixing *w* to the combinations already given.

All the five unit-character variations, which in different combinations are responsible for the color varieties of

rats, have their parallels in other mammals. Albinism and white-spotting (which in rats takes the form of the hooded pattern) are among the commonest. They occur in practically all mammals from mice to men. Albinism appears to consist in such a modification of metabolism that the process of pigment-formation can take place only feebly or not at all. That particular process which seems chiefly affected is the production of yellow pigment. Albinos, so far as I know, never produce genuine yellow pigment, though they may produce considerable quantities of black or brown pigment, as in the case of the Himalayan rabbit. An undescribed variety of guinea-pig, which I obtained about two years ago in Peru, may bear as much *black* pigment in its coat as wild cavies do, yet it forms no yellow pigment at all. Further this variation behaves as the allelomorph of ordinary albinism, indicating that it is probably of the same genetic character. For this reason *we may provisionally consider the albinism of mammals as due to a loss of the ability to form yellow pigment.* This usually, if not always, involves a lessened capacity to form other pigments also, so that it seems probable that the same chemical process, which produces yellow pigment as an end-product, is ordinarily involved also in producing the higher oxidation stages seen in brown and black pigment. In albinos this process would seem to be omitted, or to be accomplished by some step which does not involve the production of yellow pigment.

The yellow variation is extremely common in mammals. Yellow varieties, which at opposite extremes of intensity of pigmentation are known as *cream* and *red,* occur among horses, cattle, hogs, cats, dogs, rabbits, guinea-pigs, mice and human beings. In this variation pigment oxidation stops at the yellow stage, usually throughout the coat but not in the eye. Described in negative terms a yellow variety is one in which black and brown are suppressed or restricted. Black and brown, though usually restricted to the *eye* in yellow varieties, may occur also in

small quantities in the fur. Examples are found among horses (bay and dun varieties), cattle (the Jersey breed), dogs (the common dirty yellow variety), rabbits (the "tortoise-shell" variety), mice and guinea-pigs, and probably red-haired human beings also.

Black varieties of mammals arise in two genetically distinct ways. One is a quantitative increase or extension of black, the reverse of what happens in yellow varieties, so that black encroaches on regions normally yellow or may even obliterate them altogether. Examples are found in black squirrels, in which the agouti yellow ticking of the fur is almost, but not quite, obliterated by black pigment. But the "black" variation of rats, mice, guinea-pigs and ordinary rabbits results from a total loss, not a covering up, of the yellow ticking of the fur seen in agouti varieties. Genetically it is quite distinct from the other kind of black. It is a recessive variation and so breeds true.

The *pink-eyed* variation is the rarest of all the five enumerated as occuring in rats. It has been known heretofore only in mice, though I have recently obtained it also in guinea-pigs from Peru, where it seems to be well established.

In this variation the capacity to form yellow pigment is unimpaired, but only *traces* of black or brown pigment are produced. Consequently varieties which possess the other genetic factors of normal yellow animals have fully pigmented (yellow) fur, but with very faintly pigmented (pink) eyes, when they possess this factor. If, however, they possess the other genetic factors of black, brown, or agouti varieties, along with this pink-eyed variation, then both the fur and the eyes are very faintly pigmented. From this results the seeming paradox that pink-eyed blacks are less heavily pigmented than pink-eyed yellows, so that in rats the fanciers have called the former "creams," the latter "fawns."

When pink-eyed animals are crossed with albinos, offspring fully colored (eyes and all) result, as was first

shown by Darbishire some ten years ago. This indicates that the two variations are not only genetically distinct, but are physiologically complementary. The albino has defective metabolism for producing yellow (and in consequence brown and black also); the pink-eyed animal has the full mechanism for forming yellow, but its brown and black producing mechanism is defective. Together they possess the full mechanism of normal color production. Hence the reversion on crossing.

White spotting is clearly due to neither of the above modifications, but to a different change in the metabolism so that no pigment at all is produced. For an albino rabbit or guinea-pig may, as already observed, bear considerable black or brown pigment, but a white spot either on an albino, on a pink-eyed animal, or on a fully colored animal is entirely devoid of pigment. The paradox of a white spot on an albino is obtainable by crossing a white-spotted colored race with an albino race, which develops some pigment in the fur, as for example the Himalayan race of rabbits and guinea-pigs. In this way English-marked Himalayan rabbits and spotted albino guinea-pigs have been produced in my laboratory.

Postscript: While this paper was in press, Mr. Tilling, in reply to a further inquiry, wrote that his original black-eyed yellow rat was caught on a ship at Liverpool. The fact that the pink-eyed variety was found in the same general region leads him to believe that both variations were introduced on ships from some foreign country. It would be of much interest to know from what country or countries. Any information on this point obtainable from rat-catchers or others would be welcome.

"DOMINANT" AND "RECESSIVE" SPOTTING IN MICE

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Introductory

The inheritance of spotting has long proved of interest to animal geneticists. The nature of spotting is such as to afford an excellent chance to observe quantitative fluctuation and variations of very minute size. Furthermore, the fact that spotted varieties are found in all the rapidly breeding smaller domesticated mammals has led to a widespread investigation of its phenomena of inheritance.

One of the most clean-cut and constant types of spotting which has been studied is that of the "hooded" pattern in rats. This character was studied independently by Doncaster (1905) and by Castle and McCurdy (1907). All these observers agree that this form of spotting is due to a recessive Mendelizing unit which gives a 1:3 ratio in crosses with self-colored races.

In mice there has been no such well-localized pattern recorded and a series of spotted forms has been described which vary from black-eyed whites on one end of the series to heavily colored animals having only a few white hairs on the forehead or on the belly at the other extreme.

Cuénot, who did considerable work on the inheritance of spotting in mice, came to the conclusion that spotting is due to a group of recessive spotting factors which he describes as *p*1, *p*2, *p*3, *p*4, etc. His figures, however, show a single unit character difference as 3:1 and 1:1 ratios prove.

Up to 1908 all the spotting in mice was classed as recessive to solid-colored coat. At that time, however,

Miss Durham described the appearance of dominant spotting in addition to the recessive form which she also had experimented with. Such a dominant form of spotting is supposed, by Bateson, to be due to the addition of some factor for restriction of pigment formation in certain areas. This produces a dominant form of spotting as contrasted with the recessive type, which, he holds, is due merely to the loss of the "self" factor.

Hagedoorn (1912) gives data to show that the dominant form of spotting occurs in mice and in addition considers it as produced by a factor analogous to that which produces the dominant "English" spotting in rabbits.

The object of this paper is to present certain evidence concerning the nature of dominant and recessive spotting in mice; to discuss in its light the results of the above-mentioned investigations; and to criticize one additional point in Hagedoorn's work with mice.

Experimental

Materials.—Among several wild mice caught during the spring of 1911 was one individual with a white spot or "blaze" on the forehead between the eyes. This spot or "blaze" was about one quarter of an inch in length and one eighth of an inch in width. This mouse, an adult male, was transferred to a breeding cage and a series of experiments was started to determine whether the "blaze" character was inherited and, if so, in what way. As at that time no adult wild females were available from unrelated stock the wild "blaze" male (*S*1) was crossed with a female from a dilute brown race. In many ways this dilute brown race was the best possible material for such a cross. It was very closely inbred, being descended from a single pair of animals, progeny of which had been free from out-crossing for more than a year. Further, it had never given, nor has it ever given in hundreds of young, an animal with the slightest trace of a spot, even on the tail, where white bands are frequently seen in wild mice. Besides this the race was vigorous and active and yet easy to handle.

RESULTS

As a result of mating *S*1 "blaze" with a female of this dilute brown race, two litters, totalling eight young, were produced. All these young were self-colored without a trace of white, and, as expected, all resembled the male in coat color.

The F_1 generation selfs were then crossed in two ways, (1) *inter se* and (2) with animals of the dilute brown self race to which their mother belonged. It is hoped that a detailed account of all the matings made may be published later, but for the present purposes certain of the crosses under the first heading will suffice.

When F_1 was crossed *inter se*, two sorts of young were produced, namely, those with white and those without. While all of the latter type may be classed as self, the former were of two general sorts: (1) those with a "blaze" as large or larger than that of *S*1, these we may call "blaze" animals; and (2) those with only a *few white hairs* on the forehead, which we may call few white-haired (f.w.h.) animals.

The exact numbers in this cross were

Parents	Offspring		
	Self	F.W.H.	Blaze
*S*6 × *S*5—*S*8	11	3	3
*S*19 × *S*8	10	13	6
*S*18 × *S*8	3	1	2
	24	17	11

When the F_2 few white-haired animals were bred together they produced three types of young: *few white-haired, blaze* and *self,* as follows.

Parents	Offspring		
	Self	F.W.H.	Blaze
3,030 × 3,028	11	6	—
3,043 × 3,028	5	5	1
	16	11	1

One further fact is also of interest. Various descendants of F_2 "blaze" animals, which should breed as recessives,

have given the following results. The generation numbers may be disregarded as they refer to another method of classification. It is to be remembered that the parents in the tabulation given below, are all "blaze" in character.

Generation	Young Produced				
	Blaze	Blaze and Ventral White	F.W.H.	Self	Total
F_3B	33	6	4	1	44
F_4B	157	60	27	3	247
F_5B	70	53	5	0	128
F_6B	9	6	0	0	15
Total	269	125	36	4	434

If the "blaze" is a true Mendelian recessive we should expect all 434 offspring to have some white on them. The figures show that 430 of the 434 are of this type; that is to say, approximately 1 per cent. are self.

It is possible to account for the occasional production of selfs even if the "blaze" character is a true recessive, if we supposed that there are supplementary factors which may influence color development; and it is quite conceivable that such is the case.

The chief point of interest in the crosses given above is that while spotting behaves in F_1 *as a recessive, certain of the* F_2 *spotted individuals fulfil the requirements of dominant spotting by producing self offspring.*

The spotting came from a single individual and can scarcely be considered to be of two distinct types.

We may now consider the bearing of these results on the work of Miss Durham and Hagedoorn.

Miss Durham's Results

Miss Durham (1908) gives a detailed account of a recessive type of spotting in mice. The numbers she obtained are extensive, and the case seems well established, coming as it does in corroboration of the work of Cuénot, Darbishire and others. In the same papers she records the occurrence of a *dominant* spotted type of mice. Bateson (1909), commenting on the case, compares it with the

dominant "English" spotting in rabbits but also agrees that, in the case of mice, there is no criterion to enable one to distinguish somatically between the dominant and recessive forms. This, of course, is not the case in rabbits where the "English" pattern differs visibly from the "Dutch" spotting, which Hurst (1905) found to be recessive to self. Bateson also considers that the case of dominant spotting in mice, reported by Miss Durham, is the result of a different spotting factor from that producing recessive spotting.

In terms of the presence and absence hypothesis this means that the dominant form possesses a factor for restriction of pigmentation *which self forms lack.* This fact becomes of interest when Miss Durham's experimental results are closely examined.

In the race which gave rise to the dominant spotting the following conditions are seen.

A sooty yellow spotted mouse of unknown origin was crossed with a black-eyed white (spotted) animal (of Atlee's strain). Among other progeny was obtained a black-eyed white mouse with "agouti ears." This mouse, No. 21 (spotted), was crossed with an albino (carrying chocolate), No. 35, and gave among its progeny No. 69, *a black self mouse.* This black animal, No. 69 was crossed with an albino (carrying chocolate), No. 34, and from these two individuals came the dominant spotted race.

Now inasmuch as No. 34 and No. 35, the albinos, were not supposed to carry spotting, the dominant spotting must be considered as probably coming from No. 69, a *black self animal.* We know that *this animal must carry spotting as a recessive character* since its parent, No. 21, was spotted.

If, therefore, this animal was the progenitor of the dominant spotted race, and if he carried a recessive spotting, as it seems certain he did, we must suppose that one of three things has happened to the recessive spotting which he carried.

1. It may have been completely lost, failing to manifest itself in his germ cells.

2. It may have continued to exist and to be inherited together with the dominant type of spotting.

3. It may have been changed to a so-called "dominant" type of spotting simply by the nature of modifying supplementary factors which it encountered during ontogeny.

The first two cases necessitate the origin of the "dominant" spotting by a mutation in no way connected with the previous recessive spotting. In the first case, moreover, we should have to suppose the disappearance of the recessive spotting character in a manner entirely contrary to any principle of Mendelian heredity. In the second case the occurrence of the two types of spotting side by side in the same litters of young would so complicate the experiments that analysis would be difficult if not impossible, on Miss Durham's results.

There is good reason to believe that the third possible explanation is the correct one. It accounts for the formerly "recessive" type of spotting. It presupposes no fundamentally different appearance of the two types of spotting. Moreover, it is very probable that the albino race brings in the modifying factors necessary to give the apparent change in the type of spotting. The addition of a factor as presupposed by the presence and absence hypothesis is not proved by the results obtained nor is it necessary to account for them.

That the presence and absence hypothesis does not apply to all cases of spotting is seen in the case of the "blaze" mice in my experiments. Here, if F_1 animals had been given me as a starting point for experimentation, I should conclude the spotting to be recessive, while if F_2 spotted animals were given as a starting point the conclusion would be inevitable, that spotting should be considered dominant. Yet it is one and the same spotting in both cases. It is certain that "self" and "blaze" are alternative conditions, but it is equally certain that they differ from each other rather as two degrees of a

single process, one greater, the other less, than as the presence and absence of one or more unit characters.

Hagedoorn's Work

Hagedoorn's work shows the danger of the modern tendency to produce factors upon the slightest provocation. While adding, in experimental work, only a single litter of young bearing on the problem, he gives a symbol for a factor for dominant spotting in mice, and further considers it as due to a factor similar to that producing the dominant "English" spotting of rabbits. He refers to Morgan's work with black-eyed white and self mice as being a study of this dominant factor in mice. Morgan himself suggests that if black-eyed white mice represent the extremes of the spotted series the appearance of spotted animals in crosses with selfs is due to a *strengthening* of the spotting factor or to a *change* in dominance. This is far different from supposing the addition of an entirely new inhibiting factor comparable to the English pattern in rabbits. Cuénot with mice and Castle (1905) with guinea-pigs have shown that black-eyed whites *are* the extreme of the recessive spotted series and it is almost certain that Morgan's explanation of the results, as due to *a change in dominance*, is the correct one. It is, of course, obvious that the presence and absence hypothesis fails to explain any change of dominance of a single character.

To treat "dominant" spotting in mice as due to the presence of a definite unit-character is exceeding present experimental facts, while to consider it similar in nature to the "English" spotting of rabbits is still less justified.

One other point in Hagedoorn's work is of such a nature as to require further experimentation before it can be accepted.

This is the case (on page 126) of "mutual repulsion between two factors." In this case, Hagedoorn mated together agouti animals heterozygous in factor A (for color production) and in factor G (for the agouti pattern).

Such animals would ordinarily form gametes *AG, Ag, aG* and *ag* in equal numbers. These by independent recombination would form

$$\left.\begin{matrix} 1\ AAGG \\ 2\ AaGG \\ 2\ AAGg \\ 4\ AaGg \end{matrix}\right\}\text{9 agouti,}$$

$$\left.\begin{matrix} 1\ AAgg \\ 2\ Aagg \end{matrix}\right\}\text{3 black,}$$

$$\left.\begin{matrix} 1\ aaGG \\ 2\ aaGg \\ 1\ aagg \end{matrix}\right\}\text{4 albino.}$$

But Hagedoorn gives figures which show that the proportion which he obtains is nearer 2 agouti; 1 black and 1 albino. This he supposes to be due to the fact that *A* and *G* can never go into the same gamete.

Now let us see what happens if this is the case. The original heterozygotes will form only two kinds of gametes instead of four, these will be *aG* and *Ag*. Now in the recombination of these gametes the following result will be obtained.

1 *aG aG* = 1 albino,
2 *aG Ag* = 2 agouti,
1 *Ag Ag* = 1 black.

So far, so good, but the trouble comes in testing the albinos. Here I may quote from Hagedoorn, p. 126:

> . . . thirteen of these albinos have been tested by mating with black. Without exception they have given black or equal numbers of black and albino young. . . . *But never has one of those albinos produced a single agouti young in a mating with black. Counting together the colored young of such families I get 89 black young.*[1]

This result is indeed remarkable, *for on Hagedoorn's own hypothesis* the albinos should have produced in such matings *nothing but agouti young,* "since they are all, by his hypothesis, homozygous for the agouti factor. The evidence is incontestable; *no repulsion of A and G can have occurred.* Has there been any coupling of these two factors? If such was the case only gametes *AG* and

ag would have been formed and this would have given only *agoutis and albinos* in a 3:1 ratio, while Hagedoorn reports "73 agouti, *37 blacks*[1] and 32 albinos."

The case then is nothing so simple as "repulsion" or "coupling," it includes *failure to segregate and complete disappearance of a dominant Mendelian factor; G the factor for agouti.*

Since numerous investigators of color inheritance in mice have never found the agouti factor anything but a normal Mendelizing factor epistatic to black, and since Hagedoorn himself seems to have become mixed in his interpretation, it seems that the case proves or shows little until a satisfactory answer can be found to the question of what has become of the agouti factor.

Conclusions

The facts above given lead to the following conclusions:

1. The so-called dominant type of spotting in mice does not differ from "self" color by the presence of a unit character which "self" lacks. The presence and absence hypothesis fails to account for the shifting dominance seen in spotting in mice.

2. It is misleading to describe, under the same symbol, the so-called "dominant" spotting of mice and the English spotting in rabbits.

3. It seems probable that differences in "dominance" of spotting in mice are due to modifying supplementary factors and such spotting might be termed "unsuppressed" and "suppressed" spotting rather than "dominant" and "recessive" in the Mendelian sense.

4. Hagedoorn's hypothesis of repulsion between the color factor, *A*, and the agouti factor, *G*, is incorrect.

November 19, 1913.

[1] Italics mine.

ON DIFFERENTIAL MORTALITY WITH RESPECT TO SEED WEIGHT OCCURRING IN FIELD CULTURES OF PISUM SATIVUM

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In two papers which have already appeared in these pages,[1] I have shown that for the dwarf varieties of *Phaseolus vulgaris* the mortality of apparently perfect seeds (failure to germinate or to complete the life cycle) is not random, but differential, or selective.

It seemed highly desirable to extend these studies to other forms. *Pisum sativum* naturally occurred to me as affording suitable experimental material—both because of the wide range of seed characteristics and the convenience with which it may be bred. I had no pedigreed seed and consequently began work in the spring of 1913 with commercial stock. About 1,000 seeds from each of ten early (dwarf) varieties purchased from the Thorburn seed company were weighed, individually labelled and planted in short rows scattered over one of the fields of the Station for Experimental Evolution. Conditions were not the best, and the mortality was high.

Table I[2] gives the weights in units of .025 gram range[3]

[1] Harris, J. Arthur, "On Differential Mortality with Respect to Seed Weight Occurring in Field Cultures of *Phaseolus vulgaris*," AMER. NAT., 46: 512–525, 1912; "Supplementary Studies on the Differential Mortality with Respect to Seed Weight in the Germination of Garden Beans," AMER. NAT. [in press].

[2] For convenience the series may be designated by letters: *A*, Witham Wonder; *B*, American Wonder; *C*, Premium Gem; *D*, Little Gem; *E*, Nott's Excelsior; *F*, Sutton's Excelsior; *G*, Laxtonian; *H*, Little Marvel; *I*, Peter Pan; *J*, English Wonder.

[3] Class 1 = 0.000–.025 gram, . . . class 4 = .075–.100, class 5 = .100–.125, and so on. Thus to obtain means or standard deviations of weights in grams, deduct .5 from the values in the tables and multiply by .025.

TABLE I

WEIGHT OF SEEDS WHICH GERMINATED

Series	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Totals
A	1	6	31	64	65	100	75	57	42	19	6	1	1	—	—	—	—	468
B	—	—	—	—	40	107	134	170	105	35	12	1	—	—	—	—	—	604
C	—	—	3	5	53	117	173	126	56	11	3	2	—	—	—	—	—	549
D	—	—	—	3	36	106	191	167	80	18	4	1	—	—	—	—	—	606
E	—	—	—	5	49	105	105	68	32	3	—	—	—	—	—	—	—	367
F	—	—	—	—	9	27	63	96	86	69	26	11	4	—	—	—	—	391
G	—	—	—	—	1	7	27	71	114	159	132	81	23	16	—	—	—	631
H	—	—	—	1	17	44	116	183	151	63	20	6	2	—	—	—	—	603
I	—	2	—	2	6	8	16	25	51	88	127	126	101	55	17	8	1	633
J	—	—	—	17	107	126	142	112	41	13	5	2	—	—	—	—	—	565

TABLE II

WEIGHT OF SEEDS WHICH FAILED TO GERMINATE

Series	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Totals
A	4	16	49	63	102	90	93	78	42	16	2	1	—	—	—	—	—	556
B	—	—	—	2	—	52	104	117	84	36	3	—	2	—	—	—	—	400
C	—	2	1	12	56	116	122	95	34	18	4	1	—	—	—	—	—	461
D	—	—	1	5	37	88	127	93	37	11	—	—	—	—	—	—	—	399
E	—	—	—	13	115	210	180	91	23	4	1	—	—	—	—	—	—	637
F	—	—	—	—	13	46	84	125	153	114	49	16	10	3	—	—	—	613
G	—	—	—	—	5	6	29	43	75	85	70	42	13	7	—	—	1	376
H	—	—	—	1	17	66	71	110	93	29	14	3	—	—	—	—	—	404
I	—	—	3	1	13	18	26	35	29	60	65	62	31	22	3	2	4	374
J	—	—	—	13	55	88	125	91	53	12	2	—	—	—	—	—	—	439

of the seeds which germinated.[4] Table II gives the same distributions for the seeds which failed to germinate. The physical constants[5] with their probable errors are given in Tables III–IV.

Taking the differences, germinated *less* failed, in order to have the positive sign if elimination tends to increase mean weight or variability of weight and the negative sign if it tends to decrease these constants in the population of seeds which grow as compared with those which fail, I find the differences shown in Table V.

[4] When the plantlets were about three inches high the labels for seeds which had failed to germinate were collected. The distributions for the seeds which had germinated were then obtained by subtraction from the weight seriations prepared before planting. Some of the plants subsequently died.

[5] Sheppard's correction was applied to the second moments.

TABLE III

PHYSICAL CONSTANTS FOR SEEDS WHICH GERMINATED

Series	Mean and Probable Error	Standard Deviation and Probable Error	Coefficient of Variation and Probable Error
A	9.254 ± .062	2.000 ± .044	21.610 ± .498
B	10.581 ± .038	1.371 ± .027	12.954 ± .256
C	10.078 ± .037	1.294 ± .026	12.844 ± .266
D	10.355 ± .033	1.211 ± .023	11.692 ± .230
E	9.790 ± .042	1.193 ± .030	12.185 ± .308
F	11.568 ± .054	1.571 ± .038	13.583 ± .334
G	13.090 ± .043	1.612 ± .031	12.313 ± .237
H	11.186 ± .037	1.362 ± .026	12.178 ± .240
I	14.269 ± .057	2.134 ± .041	14.958 ± .290
J	9.773 ± .040	1.429 ± .029	14.622 ± .300

TABLE IV

PHYSICAL CONSTANTS FOR SEEDS WHICH FAILED TO GERMINATE

Series	Mean and Probable Error	Standard Deviation and Probable Error	Coefficient of Variation and Probable Error
A	8.993 ± .057	2.003 ± .041	22.286 ± .472
B	10.898 ± .041	1.236 ± .030	11.346 ± .274
C	9.913 ± .045	1.439 ± .032	14.512 ± .329
D	10.048 ± .041	1.229 ± .029	12.234 ± .296
E	9.488 ± .030	1.122 ± .021	11.826 ± .227
F	11.726 ± .045	1.653 ± .032	14.097 ± .277
G	12.816 ± .062	1.787 ± .044	13.945 ± .350
H	10.869 ± .049	1.447 ± .034	13.317 ± .322
I	13.225 ± .089	2.552 ± .063	19.298 ± .493
J	10.009 ± .044	1.376 ± .031	13.749 ± .311

TABLE V

COMPARISON OF PHYSICAL CONSTANTS FOR SEEDS GERMINATING WITH THOSE FOR SEEDS FAILING TO GERMINATE

Series	Difference in Mean and Probable Error of Difference	Difference in Standard Deviation and Probable Error of Difference	Difference in Coefficient of Variation and Probable Error of Difference
A	+ .261 ± .085	−.003 ± .060	−1.676 ± .686
B	− .316 ± .057	+.134 ± .040	+1.608 ± .375
C	+ .165 ± .058	−.144 ± .041	−1.669 ± .423
D	+ .307 ± .053	−.019 ± .037	− .542 ± .375
E	+ .302 ± .051	+.071 ± .036	+ .358 ± .382
F	− .158 ± .070	−.082 ± .049	− .513 ± .434
G	+ .274 ± .075	−.175 ± .054	−1.632 ± .422
H	+ .317 ± .062	−.085 ± .044	−1.139 ± .401
I	+1.044 ± .105	−.418 ± .074	−4.340 ± .572
J	− .236 ± .060	+.053 ± .042	+ .873 ± .432

Consider first the differences in the mean weight. Seven are positive and three are negative. All of the

seven positive differences are at least 2.5 times their probable error; four of them are over five times their probable error. The mortality is therefore almost certainly selective, with a tendency to leave the surviving population with seeds distinctly heavier on the average than those which were planted. On the other hand, there are the three cases in which the seeds which produced plantlets were on the average lighter than those which failed to germinate. One of these differences is only 2.2 times its probable error, and so perhaps not statistically trustworthy. Of the other two, one is over 5.5 times and the other nearly 4 times its probable error. There can be little doubt that in at least one of these cases there is a tendency for the lighter seeds to show a viability greater than that of the heavier. In garden beans, too, strong evidences of differences between strains in this regard have been pointed out.

The interpretation of the variabilities offers greater difficulties than does that of the means. More data and more refined methods of analysis are necessary for a final solution of the problem. It appears, however, that in seven of the ten series the variability of the seeds which survived is less than that of those which failed. This is true whether absolute variability as measured by the standard deviation or relative variability as expressed by the coefficient of variation be used in the comparison.

As far as these data go, therefore, they are in general accord with those for *Phaseolus*. In both of these Leguminosæ the mortality which occurs before germination is not random but differential. But in both cases, and especially in *Pisum* where the seeds used are of commercial, not pedigreed, stock and number as yet only about 10,000, far wider series of experiments and much refinement of methods of analysis are necessary to establish fully the nature and the immediate (physical or chemical) cause of this selective death rate.

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THE INHERITANCE OF A RECURRING SOMATIC VARIATION IN VARIEGATED EARS OF MAIZE[1]

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Introduction

The inheritance of variegation has special interest and importance in genetics. It is with forms of variegation that the only two certainly known cases of non-Mendelian inheritance have had to do. I refer to Baur's experiments with *Pelargonium,* in which crosses of green-leaved and white-leaved forms exhibited somatic segregations in F_1 that bred true in later generations, and to Correns's work with *Mirabilis,* which showed green and white leaf color, to be inherited through the mother only. De Vries's conception of "ever-sporting" varieties was apparently founded largely upon the behavior of variegated flowers in pedigree cultures, from which he reached the conclusion that the variegated color pattern and the monochromatic condition arising from it as sports are non-Mendelian in inheritance. Correns, however, has shown that in *Mirabilis jalapa* the inheritance of these sports is distinctly Mendelian, and the results of East and Hayes indicate the same for *Zea mays.* In this paper I shall present data from maize and attempt to show how they can be interpreted in strictly Mendelian terms.

Variegation is distinguished from other color patterns by its incorrigible irregularity. It is perhaps most often seen in the coloration of flowers and leaves but also occurs in fruits, seeds, stems, and even roots of various plants. It is characteristic of the ears of certain varieties of maize known, at least in the Middle West, as "calico" corn. In

[1] The experimental results reported here were presented at the Cleveland meeting of the American Society of Naturalists, January, 1913. Research bulletin No. 4 of the Nebraska Agricultural Experiment Station.

these varieties the pericarp of most of the grains has few to many narrow stripes of dark red, the remaining area being colorless or showing a sort of washed-out red. Often broad red stripes appear on some grains, a single stripe covering from perhaps one tenth to nine tenths of the grain. Not uncommonly there are entirely colorless grains (so far as pericarp is concerned) and also solid red grains scattered over the ear. Much more rarely there is found a "freak" ear with a large patch of self-red or nearly self-red grains. Or sometimes an ear is composed largely of red or almost red grains with a small patch of striped or nearly colorless grains. In such cases it is not uncommon for the margin of the red area to cut across a grain so that one side—always the side toward the red patch—is red and the other side colorless or striped. Ears that are colorless throughout, except for a single striped grain, are not unknown and there are even known ears that are red except for a single striped grain. Very rarely a plant has one self-red ear and one variegated ear on the same stalk. It is also conceivable that all the ears of a plant might thus become red, but of course such a red-eared plant rising as a bud-sport could not ordinarily be distinguished from a red-eared plant arising as a seed-sport.

Variegated ears generally have variegated cobs, the amount of red in the cob ordinarily varying with the amount of red on the grains. In some "freaks" a part of the cob is solid red and the rest variegated. In a few such cases the red part of the cob corresponds exactly in position to the freak patch of grains. This is more frequently true when the grains of the freak patch are dark variegated than when they are self-red. In other ears there is no change in the cob corresponding to the change in the grains. The husks of variegated ears are also rather commonly variegated. In a few freak ears the red side of the ear is enclosed in reddish husks, the remainder of the husks being light striped. Red-eared plants arising as seed-sports always have solid red cobs and usually solid reddish husks.

The first account, so far as I am aware, of the inheritance of the striking somatic variations so commonly found in variegated plants was given by de Vries[2] in his discussion of ever-sporting varieties. The study was made in the years from 1892 to 1896 with a variety of *Antirrhinum* with striped flowers. De Vries's records are reproduced diagrammatically in Fig. 1.

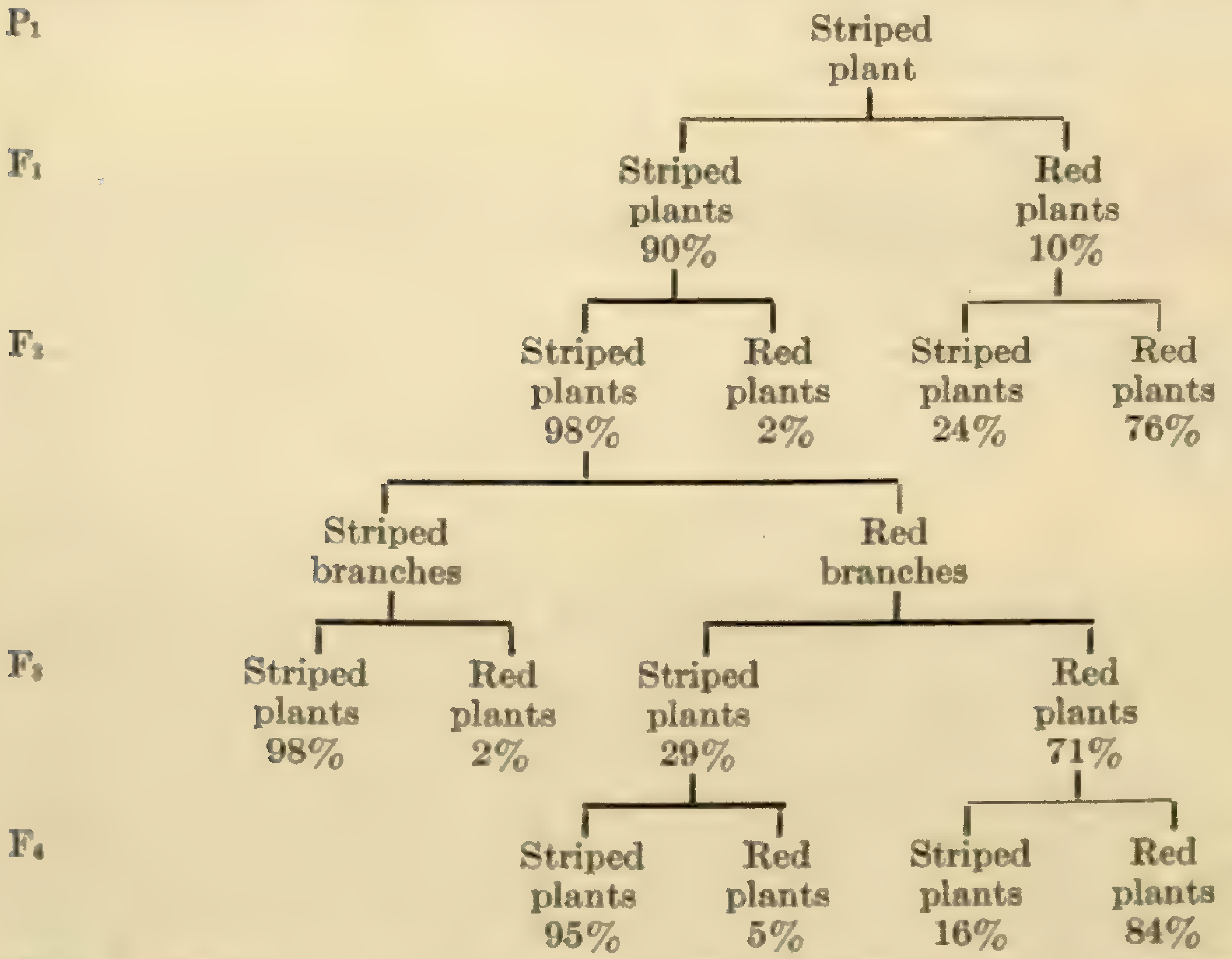

FIG. 1. DIAGRAM FROM DE VRIES'S RECORDS SHOWING THE INHERITANCE OF VARIEGATION AND SELF-RED IN THE FLOWERS OF *Antirrhinum*.

Of these results de Vries says:

From these figures it is manifest that the red and striped types differ from one another not only in their visible attributes, but also in the degree of their heredity. The striped individuals repeat their peculiarity in 90–98 per cent. of their progeny, 2–10 per cent. sporting into the uniform red color. On the other hand, the red individuals are constant in 71–84 per cent. of their offspring, while 16–29 per cent. go over to the striped type. Or in one word: both types are inherited to a high degree, but the striped type is more strictly inherited than the red one.

De Vries's results were in some respects very similar to those of Correns and it is probable that he would have interpreted them in the same way had he then been familiar with Mendelian phenomena.

[2] Vries, Hugo de, "Species and Varieties," pp. 309–328 (1905).

Correns[3] has reported results of a careful study of the inheritance of the self-green condition appearing as a bud-sport on variegated-leaved plants of *Mirabilis jalapa,* and also of a self-color appearing in striped-flowered plants of the same species. His results for self-green and variegation of the leaves are shown diagrammatically in Fig. 2. The results are stated in approximate percentages. I have seen no report in which the detailed records were given.

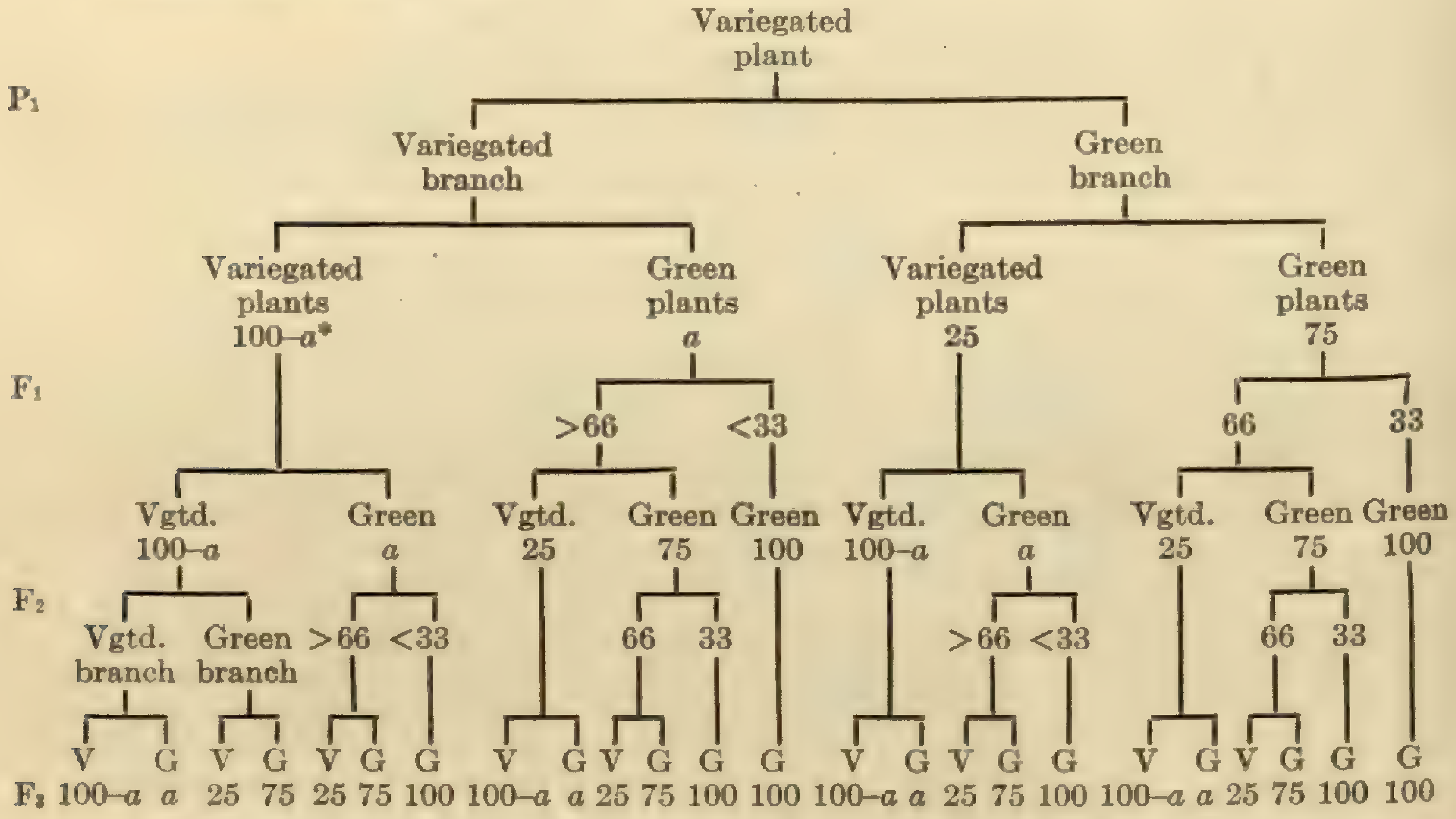

FIG. 2. CORRENS'S DIAGRAM SHOWING THE INHERITANCE OF VARIEGATION AND SELF-GREEN IN THE LEAVES OF *Mirabilis jalapa.*

The diagram shows that a variegated branch of a variegated plant produces in F_1 mainly variegated plants, but occasionally a wholly green plant, while a green branch from the same plant produces in F_1 25 per cent. variegated and 75 per cent. green plants. The F_1 variegated plants, however produced, behave in later generations just like the original variegated parent plant. The F_1 green plants, whether produced from green or variegated branches, are always of two sorts, namely, those that are homozygous and therefore breed true green, and those

[3] Correns, C., *Ber. Deutsch. Bot. Gesel.,* 28: 418–434, 1910. *Der Übergang aus dem homozygotischen in einen heterozygotischen Zustand im selben Individuum bei buntblättrigen und gestreiftblühenden Mirabilis-Sippen.*

* Numerals indicate approximate percentages; $a = 0$–10 per cent.

that are heterozygous and therefore produce progenies of green and variegated individuals in a ratio of approximately 3 to 1. Correns points out that a green branch of a variegated plant behaves as though it belonged not to a variegated plant at all, but to a hybrid between a variegated plant and a green one, in which green is dominant, and that half of the germ cells produced by the green branch carry a factor for green and the other half a factor for variegation. Similar results were secured from branches with self-colored flowers on plants with striped flowers, except that such branches produce few if any more self-colored plants than are produced by branches with striped flowers. Plants with self-colored flowers, no matter how they arise, behave as they would if they had occurred in an F_2 progeny of a cross of striped by self-colored plants.

Results of Experiments with Maize

Hartley[4] in 1902 gave an account of an experiment with variegated maize. In a comparatively pure white strain, which occasionally produced a red ear, there was found an ear similar to some of the "freak" ears noted earlier in this paper. It is described as being red except for a spot covering about one fifth of the surface, in which the grains were white with fine red streaks. The excellent plate accompanying the account, however, shows that most of the "red" grains had white streaks at the crown and that the cob was light-colored, not red. From the near-red grains of this ear there was produced a crop of 84 red ears and 86 pure white ones, while from the variegated grains of the same ear there came 39 light variegated ears and 36 white ones. Hartley refers to the parent ear as a "sport or sudden variation from the type" but does not indicate whether the "type" in mind was the white variety or the red ears occasionally produced by it. Both the color of the grains and cob and the production of about 50 per cent. of white ears from both the red and the variegated grains indicate very clearly that the parent ear was a

[4] Hartley, C. P., Yearbook, U. S. Dept. Agr., 1902: 543–544.

heterozygous, variegated one and that it probably came from a white seed crossed by a stray grain of pollen from a variegated-eared plant, just as the occasional red ears in the white variety were certainly produced by stray pollen from red-eared plants.

More recently East and Hayes[5] reported like behavior of a similarly variegated ear. An ear having on one side solid red grains and on the other white and very light variegated grains, similar to some of the "freak" ears noted earlier in this paper furnished the material for the test. The ear was produced from a white seed in a field of otherwise pure white corn and was therefore doubtless heterozygous for pericarp color and was probably pollinated in large part from plants without pericarp color, so that 50 per cent. white-eared plants were to be expected in its progeny. The white, the light variegated and the solid red grains were planted separately. The white and the variegated seeds alike produced light variegated and white ears, 15 of the former and 15 of the latter. The red seeds produced 22 white ears and 22 solid red ears. The authors' interpretation of these results is that the white seed which gave rise to the original colored ear had been fertilized by pollen from a red-eared plant and that the F_1 plant, "due to produce a red ear varied, somatically so that one half of the ear was red and one half striped." The authors further state:

> This variation was transmitted by seeds, but at the same time the hybrid character of its seeds was unchanged as shown by their segregation into reds and whites in the next generation and the normal segregation of the hybrid dark reds in a further generation.

In the light of my own observations, it is equally possible and seems more likely that the white seed from which the original red-and-variegated ear came was the result of pollination from a plant with variegated ears, and that the somatic variation was from variegated grains to solid red grains rather than from red to variegated. But the important fact is that a somatic variation was later inherited in a strictly Mendelian way.

[5] East, E. M., and Hayes, H. K., Bul. Conn. Agr. Expt. Sta., 167: 106–107. 1911.

In 1909 I obtained results somewhat similar to those reported by East and Hayes. A few "freak" ears were secured, mainly from local and national corn expositions. Nothing was learned as to their parentage or pollination. Obviously, however, the parentage of the red, the variegated, and the white grains of any one ear was the same, and it is reasonable to suppose that the different sorts of grains of any one ear were pollinated with approximately the same kind or the same mixture of pollen. The results, as shown below, were essentially like those of Hartley and of East and Hayes.

Seeds Planted	Number of Plants with		
	Red Ears	Variegated Ears	White Ears
Self-red	43	0	33
Variegated and white	0	22	29

The results from four other ears were somewhat different, probably owing to differences in their pollination. (See Fig. 3.) They were as follows:

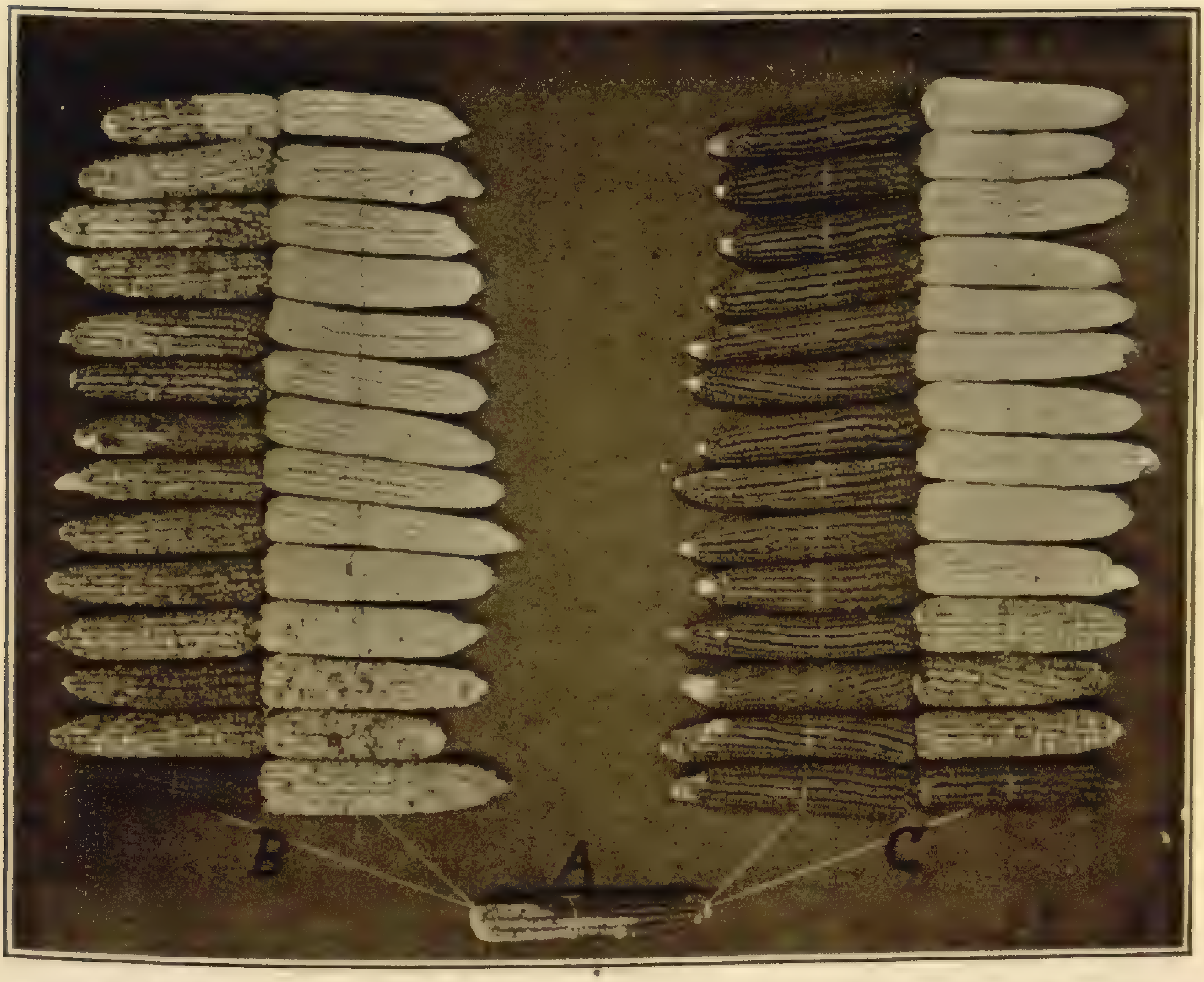

FIG. 3. *A*, "freak" ear of maize; *B*, progeny of striped seeds; *C*, progeny of self-red seeds.

Seeds Planted	Number of Plants with		
	Red Ears	Variegated Ears	White Ears
Self-red	128	32	69
Variegated and white	8	103	68

Two other ears of similar history, while they gave quite as striking results as those noted above, probably do not belong here since none of their immediate progeny were variegated and no variegated ears have occurred in later generations. These two ears were made up of red grains and white grains only. The results were as follows:

Seeds Planted	Number of Plants	
	Red Ears	White Ears
Red	77	85
White	0	122

The white ears bred true in later generations and the red ears produced reds and whites in typical Mendelian fashion. No such somatic variations as these have occurred in my cultures of self-red or white maize, so that I have been unable to study them further. Somatic variations in variegated corn, however, are not rare. Unfortunately several of the most pronounced of those occurring in my cultures were open-pollinated and therefore of little or no use in a careful study. I have therefore been obliged to make use in large part of the few solid red and nearly solid red grains scattered over otherwise more or less evenly variegated ears.

From twenty-three self-pollinated, variegated ears of plants that were homozygous for pericarp color, grains with various amounts of red were selected and planted. The results are summarized as follows:

Seeds Planted	Number of Plants with		
	Self-red Ears	Variegated Ears	Non-red Ears
Self-red	8	9	0
Nearly self-red	56	16	0
More than half red	9	34	0
Less than half red	5	22	0
Narrow red stripes	33	394	0
Non-red	1	22	0

Besides these 23 ears, 20 other selfed ears from homozygous plants contained only narrow-striped seeds from which there were produced 16 plants with red ears, 280 with variegated ears, and none with white ears. Similarly 21 selfed ears with narrow-striped seeds only, from plants that were heterozygous for pericarp color, produced 28 plants with red ears, 411 with variegated ears, and 208 with non-red[6] ears. Variously colored grains from 42 self-pollinated, heterozygous, variegated ears gave the following results:

Seeds Planted	Number of Plants with		
	Self-red Ears	Variegated Ears	Non-red[7] Ears
Self-red	15	1	6
Nearly self-red	17	8	8
More than one half red	46	51	31
Less than one half red	8	34	21
Narrow red stripes	57	767	300
Non-red	0	10	6

In the progenies of these 63 self-pollinated ears that were heterozygous for pericarp color, there were approximately 2.5 plants with pericarp color to one without it. All the classes of grains from self-red to non-red yielded both colored and non-colored ears, thus indicating, as already shown by East and Hayes, that the somatic variation in the seeds does not change their hybrid character. Considering only the plants with pericarp color, in the progenies of both heterozygous and homozygous variegated ears, 106 progenies in all, marked differences are seen in the percentages of self-red ears from seeds of the different color classes, as follows:

[6] Some of these ears had what I have termed "half-red" pericarp, *i. e.*, pericarp with a reddish color extending part way from the base to the crown of the seeds. (See Ann. Rpt. Nebr. Agr. Expt. Sta., 24: 62. 1911.) Half-red differs from self-red and variegated red not only in distribution but also in almost never developing fully in the heterozygous condition. It is hypostatic to self-red, but shows between the red stripes of variegated seeds. Since its presence does not mask either self-red or variegated-red and since it is strictly allelomorphic to both of them, half-red is here included with non-red. Variegated ears have never, in my observation, produced half-red grains as somatic variations.

[7] Some of these were half-red. See footnote 6.)

Seeds Planted	Number of Plants with		Per Cent. Self-red Among Colored Ears
	Self-red Ears	Variegated Ears	
Self-red	23	10	69.7
Nearly self-red	73	24	75.3
More than one half red	55	85	39.3
Less than one half red	13	56	18.8
Narrow red stripes	134	1,852	6.7
Non-red	1	32	3.0

In comparison with the cases reported by Hartley and by East and Hayes and one of my first cultures from open-pollinated ears, in all of which red grains produced no variegated ears and striped grains no red ones, the striking features of the results from these 106 self-pollinated ears are the facts that the wholly red grains yielded some variegated as well as red ears and that the striped grains and even the wholly non-red grains yielded some red as well as variegated ears. The percentages noted above indicate in a general way that for self-pollinated, variegated ears, *the more red there is in the seed planted the larger the percentage of red ears in the progeny.* These records, however, do not give a wholly trustworthy indication of the mode of inheritance of the somatic variations concerned here. If there is a modification of some factor in the female gametes, associated with a visible modification of somatic cells of the pericarp and even at times of the cob and husks, modifications that do not become visible until long after the gametes are formed, may there not be a similar modification of the same factor in the male gametes, though here not associated with any visible change in somatic cells because of the fact that the staminate inflorescence dies too soon after the pollen is shed? If male gametes do carry such modified factors and if the modification is as irregular in occurrence as the somatic modifications seen in variegated ears, so that any part of the tassel, from all to none, may produce gametes with the modified factor while not showing any visible somatic modification, it is obvious that the real nature of the male gametes of any variegated-eared maize plant can not be foretold. The mere fact that a variegated ear is self-pollinated, therefore, does not insure that its seeds are fertilized with pollen of known character.

That the male gametes of variegated-eared maize do often carry factors for self-red is shown by crosses of pure non-red strains with pollen from plants with variegated ears. The plants that furnished the pollen for these crosses were in some cases the same ones whose self-pollinated ears were concerned in the records discussed above. The results of these crosses are summarized here. Eight non-red ears crossed by plants that were homozygous for pericarp color yielded 17 red-eared, 116 variegated-eared and 8 white-eared[8] plants. Similarly, 14 ears of pure non-red strains crossed by pollen from plants heterozygous for pericarp color yielded 26 red-eared, 192 variegated-eared and 229 white-eared plants. Considering merely the plants with colored ears, 22 crossed ears produced 43 red-eared to 308 variegated-eared plants, or a little over 12 per cent. self-red.

Since the male gametes of variegated-eared corn have now been shown occasionally to carry a factor for self-red, it is obvious that only from crosses of variegated-eared plants with pollen from pure non-colored strains, can a definite idea of the inheritance of the somatic variations in pericarp color be gained.[9] Twelve ears from homozygous, variegated plants cross-pollinated by non-red strains might have afforded important evidence, but for the fact that 7 of them contained only narrow-striped grains and the other 5 no fully or even nearly self-red grains. The results are summarized here:

Seeds Planted	Number of Plants with		
	Self-red Ears	Variegated Ears	Non-red Ears.
More than one half red.....	5	11	0
Less than one half red......	0	15	0
Narrow red stripes.........	2	281	0
Non-red..................	0	22	0

[8] Some of the 8 white ears may have been extreme light types of variegation, for in some other cases very light variegated and wholly white ears have been observed on the same plant. And of course some of them may have been due to accidental pollination of the parent ear.

[9] Though the genetic factors for pigment patterns in maize seem to be distinct from the factors for the pigment concerned in these patterns, no non-colored maize that I have used has ever given any indication in crosses of carrying pattern factors.

The principal facts of interest here are the production of only one red-eared plant to about 140 variegated-eared ones from narrow-striped seeds, and of about one red-eared to two variegated-eared plants from seeds with from one half to perhaps three fourths red.

Of 20 variegated ears, heterozygous for pericarp color, that were crossed with pollen from pure non-colored strains, 5 had only narrow-striped grains and 15 had variously broad-striped grains and even some self-red ones. The summaries of these crosses are as follows:

Seeds Planted	Number of Plants with		
	Self-red Ears	Variegated Ears	Non-red Ears
Self-red	9	0	11
Nearly self-red	5	0	2
More than one half red	4	2	2
Less than one half red	3	5	9
Narrow red stripes	7	265	301
Non-red	0	27	20

Here again, just as with homozygous, variegated ears, *the more red there is in the pericarp the more likely are the female gametes to carry a factor for self-red.* While the number of individuals dealt with are too few to afford reliable evidence, it is suggestive to note that the ratio of red-eared to variegated-eared plants, though not the ratio of red-eared to total plants, is greater in case of parent ears that are heterozygous than of those that are homozygous for variegated pericarp.

So far nothing has been said of the results in generations later than the one grown from the selected seeds (F_1). Let us now see what results follow when the variegated ears and the red ears produced as explained above become the parents of second generations (F_2) from the selected seeds. The variegated ears so produced behave like the original variegated ears from which seeds were selected and their progenies have, therefore, been included in the data already presented. There remains only to present the records of the progenies of red ears.

Data are available from 7 F_1 red ears obtained from self-pollinated, homozygous, variegated plants. Five of

these red ears were self-pollinated and two were crossed with pure white-eared plants. The results in F_2 and F_3 were as follows:

Seeds Planted from	Number of Plants with		
	Self-red Ears	Variegated Ears	Non-red Ears
F_1 reds from selfed, homo., vgtd. P_1's			
5 ears selfed	119	37	0
2 ears × white	46	45	0
F_2 reds from selfed F_1 reds			
1 ear selfed	9	2	0
1 ear selfed	16	0	0
F_2 reds from F_1 reds × white			
1 ear selfed	26	0	5
2 ears × white	40	0	37

The above is approximately what would have been expected, had *the F_1 red ears that arose from self-pollinated, homozygous, variegated-eared plants been produced by a cross between red-eared and variegated-eared races.*

Of the F_1 reds arising from self-pollinated, heterozygous, variegated-eared plants, nine were selfed and two were crossed with whites. The results secured in F_2 and F_3 follow:

Seeds Planted from	Self-red Ears	Variegated Ears	Non-red Ears
F_1 reds from selfed, hetero., vgtd. P_1's			
3 ears selfed (a)	104	23	0
1 ear × white	6	7	0
6 ears selfed	105	0	38
1 ear × white	12	0	7
F_2 reds from selfed F_1 reds of (a)			
4 ears selfed	59	12	0
1 ear selfed	23	0	0

From the above it appears that *the F_1 red ears, arising from self-pollinated, heterozygous, variegated-eared plants behave in some cases as if they were hybrids between red-eared and variegated-eared races and in other cases as if they were hybrids between red-eared and white-eared races.*

Of the four possible sorts of red-eared "sports" from variegated-eared plants, two remain to be treated. Be-

cause of their similar behavior they will be considered together here. Of the F_1 red ears arising from homozygous, variegated-eared plants that had been crossed with white-eared races, three were self-pollinated and two crossed with whites. Of the F_1 red ears arising from heterozygous, variegated-eared plants that had been crossed with white-eared races, four were selfed. The results in F_2 and F_3 are:

Seeds Planted from	Self-red Ears	Variegated Ears	Non-red Ears
F_1 reds from vgtd. P_1's × white			
P_1's homozygous			
3 ears selfed	54	0	16
2 ears × whites	34	0	43
P_1's heterozygous			
4 ears selfed	102	0	47
F_2 reds from selfed F_1 reds			
3 ears selfed	32	0	10
1 ear selfed	43	0	0

So far as these results go they indicate that *F_1 reds arising from crosses between both homozygous and heterozygous, variegated-eared plants and white-eared races behave as if they were hybrids between red-eared and white-eared races.*

One homozygous, variegated-eared plant was cross-pollinated by a homozygous red race. From the variegated ear produced, self-red, nearly self-red, and narrow-striped seeds were planted. All resulted, of course, in red-eared F_1 plants, 16 in all. A self-pollinated F_1 red ear from a narrow-striped seed gave in F_2 24 red-eared and 11 variegated-eared plants—somewhat fewer reds than were to have been expected. An F_1 red ear from a nearly self-red grain, when cross-pollinated with non-red, yielded 9 reds and 11 variegated in F_2. A third F_1 red-eared plant, this one from a self-red grain of the variegated parent ear, bred true red in F_2. One ear of this F_1 plant was selfed and yielded 14 reds in F_2, and another ear was cross-pollinated by non-red and yielded 29 reds.

There are various other somatic variations rather frequently seen in maize, but they are apparently not in-

herited. There are sometimes found variegated ears with a large patch of self-red cob but with little or no corresponding change in the color of the overlying grains. I have as yet no evidence that this somatic variation in cob color is inherited through the seeds of the self-red part of the cob. Such seeds apparently always produce ears with variegated grains and variegated cobs, just as do other seeds of the same parent ear. Of course variegated seeds from a self-red patch of cob occasionally give rise to a self-red ear, as discussed in detail in this paper, and such red ears always have self-red cobs, but this is also true of all self-red ears, whether or not they are produced by red or by variegated seeds and without respect to whether the part of the cob underlying these seeds is self-red, finely variegated, or entirely white.

Another form of somatic variation seen in ears of maize is the occurrence of patches of considerable size, the grains of which, though variegated, are much darker in color than the grains of the rest of the ear. Such patches of grains are often quite as strikingly distinct in appearance as patches of self-red grains, and are apparently even more likely to correspond exactly in outline with an underlying patch of self-red cob than are patches of self-red grains. Moreover, such dark, variegated grains often present a rather definite color pattern. The crowns are often made to appear almost solid red by the widening and convergence at the crown of narrow red stripes extending down toward the base of the grain particularly on the side opposite the germ. Another type of dark, variegated grains differs from the lighter, variegated grains of the same ear principally in the greater development of the somewhat washed-out red apparently underlying the dark red stripes of the variegation pattern proper. I have grown numerous progenies from dark and light variegated grains of the same ears, but as yet have no evidence that such somatic variations are inherited. Notwithstanding this, I have strains of maize breeding true to a very dark type of variegation, others to a medium

sort of variegation, and still others to exceedingly light types of variegation. There can be no doubt that some of these different types of variegation are inherited, but the mode of inheritance in crosses has not been fully worked out.

One other form of grain coloration that might be called an extremely dark type of variegation is to be noted. The grains are self-red throughout except for a nearly colorless crown formed by converging light stripes extending some way down the side of the grain opposite the germ, almost exactly the reverse of one of the types of dark variegation described above. Variegations of this sort behave in inheritance almost exactly like fully self-red grains, giving a large percentage of red-eared progeny. And these red ears are apparently always fully self-red, never showing the pattern of converging light lines seen in the parent seeds. Many such seeds have been included in the results recorded earlier in this paper where they were listed as "nearly self-red."

Interpretation of Results

Any interpretation of the data presented here must take account of these facts: (1) that the more red there is in the pericarp the more frequently do red ears occur in the progeny, and (2) that such red ears behave just as if they were F_1 hybrids between red and variegated or red and white races. The development of red in the pericarp is evidently associated with and perhaps due to a modification of some Mendelian factor for pericarp color in the somatic cells. The zygotic formula of a plant homozygous for variegated pericarp may be designated as *VV*, and that of a plant heterozygous for variegated pericarp as *V*—. If in any somatic cell *VV*, from unknown causes, a *V* factor were transformed into a factor for self-color, *S*, that cell would then have the formula *VS*. Any pericarp cells descended from it would without further modification be red. If all the pericarp cells of a seed were thus descended, the seed would be self-red, just as it would

if the plant bearing it were a hybrid between pure red and variegated races. Moreover, one half of the gametes arising from such somatic cells would carry *V* and one half would carry *S*, just as if the plant were a hybrid of red and variegated types. Or, if both *V* factors were changed, the grains would be self-red as before, but all instead of half the gametes would carry *S*. If, however, the modification from *VV* to *VS* should occur very early in the life of the plant, or even of the embryo, all the ears of the plant might thereby become self-red, and one half of all the gametes both male and female might then carry *S* and the other half *V* as in the ordinary hybrid. Or the plant might then become a sectorial chimera with one variegated ear and one red ear, the gametes from the one side of the plant all carrying *V*. If the modification occur much later, say soon after the ear begins to form, there might then be merely a solid patch of red grains on an otherwise variegated ear. In this case only those gametes arising from these smaller masses of tissue would carry half *S* and half *V*. If, however, the modification occur after the grains begin to form, the latter might be perhaps three fourths red, or one half red, or merely have narrow stripes of red, depending upon the amount of pericarp directly descended from the modified cell. In this case it seems reasonable to assume that the larger the mass of modified tissue the greater the chance that the gametes concerned should carry *S*. Finally, if in certain grains the change never occurs, they should show no red and the gametes formed in connection with them should all carry *V*, none *S*.

Similarly, it may be assumed that in any cell of a heterozygous, variegated-eared plant, *V*—, the *V* factor may as before become an *S* factor. The effect on pericarp color would be exactly the same as in a homozygous, variegated plant, and, of the gametes arising from the modified tissue, one half would carry *S* as in the other case, but the other half, instead of carrying *V*, would carry no factor and would be represented by —.

If the interpretation suggested here is correct, it is to be expected that the more red there is in the pericarp of any seeds, *i. e.,* the larger the mass of tissue descended from the cell in which the change from *V* to *S* took place, the greater the chance that the female gametes concerned carried the factor *S*. With heterozygous, variegated-eared plants, *V*—, however, never more than half of the gametes concerned could carry *S* even in case of self-red grains, the other half of the gametes carrying no factor, —. Of the heterozygous, variegated ears the progenies of which have been reported here, some were selfed, some crossed with white, and some open-pollinated. From self-pollinated ears, self-red and nearly self-red seeds yielded 32 red-eared, 9 variegated-eared, and 14 non-red-eared plants, or practically 58 per cent. self-red. This excess of self-red ears may be due, in part at least, to the presence of the *S* factor in some of the male gametes concerned, but the numbers are too small to give very reliable indications. From similar ears that instead of being selfed were crossed with white, so that the results could not have been influenced by factors present in the male gametes, self-red and nearly self-red seeds produced 14 plants with red ears and 13 with non-red ears, or about 52 per cent. red. While these numbers are very small, the fact that no variegated ears were produced, but that every ear with any red color was self-red, is noteworthy. From the open-pollinated, heterozygous ears included in my cultures self-red seeds gave progenies consisting of 171 red-eared, 32 variegated-eared, and 102 non-red-eared plants, or about 56 per cent. red.

In case of homozygous, variegated-eared plants, *VV*, all the gametes associated with seeds that later become self-red could carry *S* only if both *V* factors of the somatic cells from which the gametes arise were changed to *S* factors. Because of the rarity of changes from *V* to *S*, unless both *V* factors are influenced alike by whatever causes the change, so that both change simultaneously to *S* factors, the chance is slight that more than one will ever change.

In the latter case only about 50 per cent. of the gametes associated with self-red grains of homozygous, variegated ears could be expected to carry *S*, just as in the case of heterozygous ears. None of the open-pollinated ears whose progenies I have grown were homozygous for variegated pericarp, and none of the homozygous ears that had been crossed with white contained any self red or nearly self-red seeds. The only data, therefore, that bear upon the point at issue are those obtained from self-pollinated, homozygous, variegated ears. The self-red and nearly self-red seeds of such ears produced 64 red-eared and only 25 variegated-eared plants, or about 72 per cent. self-red. This may mean that in some cases both *V* factors were changed to *S* factors, but the results may just as likely be due to the presence of *S* in an unusually large percentage of the male gametes concerned. The production of the 25 variegated-eared plants, however, is very good evidence that, in at least a very considerable number of cases, not more than one of the two *V* factors could have been changed to *S*.

If the change from *V* to *S* should happen to occur at such a time that the grain rudiments became sectorial chimeras consisting of say one half modified cells and one half unmodified ones, one half of the pericarp would be expected to show red color and the other half no color. It would be expected further that the chances of a particular gamete's arising from a modified or from an unmodified cell would be equal. If then one half of the gametes associated with these one-half-red grains arise from cells in which only one of the *V* factors has been changed to *S*, one fourth of the gametes should carry *S* and three fourths should carry *V*, or one fourth *S*, one fourth *V*, and one half —, depending upon whether the ears concerned are homozygous or heterozygous for variegated pericarp. Such grains from homozygous ears should, therefore, whether selfed or crossed by white, yield about one red ear to three variegated ones. Similarly, from heterozygous ears, grains with one half their pericarp red should

yield about one red to two variegated to one white if self-pollinated and one red to one variegated to two white if crossed by white. (This is on the assumption that no *S* factors are carried by the male gametes.) Let us assume that by lumping together all the seeds listed in the foregoing records as "more than one half red" and as "less than one half red" the whole lot would average about one half red, and compare the results with the expectation as noted above. From grains of these two classes from homozygous ears both selfed and crossed by white, there resulted 19 red-eared and 82 variegated-eared plants, or a ratio of about 1:4.3 instead of 1:3. From heterozygous ears self-pollinated grains of these two classes yielded 54 red-eared, 85 variegated-eared, and 52 white-eared plants, and similar grains crossed by white yielded 7 red-eared, 7 variegated-eared, and 20 white-eared plants, or ratios of 1.04:1.63:1 and 1:1:2.86 instead of 1:2:1 and 1:1:2, respectively. The observed ratios are certainly suggestive but must not be given undue importance, for there is no assurance that the seeds used really averaged one half red and no assurance that some of the male gametes in the case of the selfed seeds did not carry *S*.

We must now examine the results secured in generations later than F_1, and note whether the hypothesis under consideration applies equally well to them.

It will be recalled that F_1 red-eared plants that arose from homozygous, variegated ears which had been self-pollinated (see page 99) yielded in F_2 only red-eared and variegated-eared progeny. On our assumption the formula of the parent variegated ears was *VV*, but the red grains of these ears were *VS* and the gametes associated with them therefore either *V* or *S* or all *S*. Female gametes carrying *S* would have produced red ears in F_1 whether the male gametes carried *S* or *V*, and female gametes with *V* could not have produced red ears except when the male gametes uniting with them carried *S*. The F_1 red-eared plants must therefore have been *VS* or *SS*, the former being expected much more frequently than the

latter, owing to the rarity of S in male gametes. Only 7 such red ears were tested and all yielded red and variegated ears in typical Mendelian ratios, showing that all of them were VS like any F_1 hybrid between red and variegated races. Of two F_2 reds from selfed F_1's, one again yielded reds and variegates and one apparently bred true red. Three F_2 reds, from F_1 reds crossed by whites, yielded reds and whites only—typical Mendelian results throughout.

When F_1 red-eared plants arose from either homozygous or heterozygous, variegated ears that had been cross-pollinated by whites they yielded only red-eared and white-eared, never variegated-eared, offspring (see page 100), just as if they were F_1 ears of a cross of reds with whites. By hypothesis the parent variegated-eared plants were V— and VV, and their red grains S— and SV (or possibly SS). The gametes associated with such grains were therefore S and —, and S and V (or possibly all S). The male gametes from white races were all —. The F_1 plants were therefore S—, V—, and — —, only those with S— having red ears. The five red-eared F_1 plants that were tested produced in F_2 red-eared and white-eared plants in Mendelian ratios. Of the F_2 red-eared plants one bred true in F_3 and three again segregated into reds and whites.

When heterozygous, variegated, parent ears were self-pollinated, the F_1 red-eared plants behaved in some cases like hybrids of red with variegated races and in other cases like hybrids of red with white races (see page 99). Our assumption is that the variegated-eared parent plants were V— and their red grains S—. The gametes associated with these red grains were of course S and —. The male gametes of the same plants were doubtless largely V and —, though a few were probably S. The F_1 plants must therefore have been — —, V—, S—, SV or SS. Reds with SS would be expected only rarely, and of the 11 F_1 reds tested none had that formula, else they would have bred true in F_2. Seven of the 11 F_1 reds evidently were

S—, for they yielded F_2 progenies consisting of reds and whites only. Four of the 11 were obviously *SV*, for they yielded F_2's of reds and variegates only. Of the latter F_2 reds, one bred true in F_3 and four again segregated into reds and variegates.

From a self-red seed of a homozygous, variegated ear that had been cross-pollinated by a pure red race, an F_1 red-eared plant was produced and this plant bred true red in F_2. From a nearly self-red seed of the same variegated, parent ear, an F_1 red was produced but yielded reds and variegates in F_2 just as did a similar F_1 ear from a seed with narrow red stripes (see page 100). The variegated parent ear was *VV* and the red and near-red grains probably *VS*. The gametes associated with these grains were *V* and *S*. The male gametes were all *S*. Therefore the F_2 reds were in part *VS* and in part *SS*.

By way of summary, it is recalled that, in all, 28 F_1 red-eared plants were tested by F_2 progenies. Only one of these bred true and that one came from a red grain of an ear that had been cross-pollinated by a pure red race. Disregarding the three F_2 red-eared plants thus produced and the 9 red ears produced from seeds of variegated ears that had been cross-pollinated by white races and that therefore could not have bred true, there remain 16 F_1 reds, none of which bred true in F_2. Had these F_1 red-eared plants behaved as did the F_1 green-leaved plants produced by green branches of variegated-leaved parents in Correns's experiments, approximately 5 of the 16 should have bred true. It will be recalled that Correns found that such green branches always produced green-leaved and variegated-leaved plants in the ratio of 3:1, and that one of the three bred true and the other two again segregated, just as must have happened if the green branch had been a part of an F_1 hybrid of green with variegated instead of a part of a homozygous variegated plant.

The difference between *Zea* and *Mirabilis* is, however, not a fundamental one, but is due merely to the circum-

stance that *Mirabilis* has perfect flowers while *Zea* is monecious. In *Mirabilis* both male and female gametes of a green branch arise from somatic cells in which the *V* factor has changed to a *G* factor. If a change in only one *V* factor is responsible for the production of the green branch, the somatic cells of such a branch must all be *VG* and the results reported by Correns are the only ones to be expected. With *Zea mays,* however, all the grains of one ear of a variegated-eared plant might arise from cells having *VS,* so that half of the female gametes would carry *S,* while little or no corresponding change might take place in the staminate inflorescence and therefore no (or very few) male gametes would carry *S*. From such an ear of maize only about one half, instead of three fourths, of the F_1 plants should have red ears and none (or very few), instead of one third, of the F_1 plants should breed true.

The occasional green plants ("*a*" per cent.) arising from variegated branches in Correns's experiments with *Mirabilis* are more nearly comparable to F_1 red-eared maize plants than are the green plants arising from green branches. It is quite conceivable that on a variegated branch the male gametes might arise from cells that are *VG,* while the female gametes arise from cells that are *VV,* or the reverse, though this difference between male and female gametes would hardly be so common an occurrence as with maize where the staminate and pistillate inflorescences are situated so far apart. It is worthy of note in this connection that of the occasional green plants produced by selfed seed of variegated plants in Correns's experiments with *Mirabilis* (see diagram, Fig. 2), less than one third bred true and more than two thirds segregated into green and variegated. (Correns indicates this merely by the signs $<$ and $>$ in connection with 33 per cent. and 66 per cent. respectively, in his diagram, and gives no indication of how much less than 33 per cent. bred true or how much more than 66 per cent. segregated.)

De Vries's results with *Antirrhinum* yield readily to

the same analysis used with *Zea* and *Mirabilis*. Selfed seed from striped-flowered branches gave a small per cent.—from 2 to 10—of red-flowered plants. Only a few of the red-flowered plants were tested and these were found to yield 76 per cent. red to 24 per cent. striped. Selfed seed from red-flowered branches of striped-flowered plants yielded 71 per cent. red-flowered and 29 per cent. striped-flowered plants, approximating the 75 per cent. and 25 per cent. indicated by Correns's results with *Mirabilis*. None of these red-flowered plants bred true, but only one test, and that of only a few plants, was made. The results were 84 per cent. red-flowered and 16 per cent. striped-flowered plants. It seems quite likely that had de Vries tested more red-flowered plants he would have found some of them to breed true.

Correns's results with striped and red flowers of *Mirabilis* differed in one important respect from his results with variegated and green plants of the same species, as well as from the principal results with *Zea* reported here and from de Vries's results with striped-flowered and red-flowered forms of *Antirrhinum*. When red-flowered plants arose from striped-flowered varieties of *Mirabilis*, they behaved just as did the green plants that arose from variegated forms. But selfed seeds from wholly red-flowered branches of otherwise striped-flowered plants yielded little if any larger percentages of red-flowered plants than did selfed seeds from striped-flowered branches of the same plants. It would seem that in case of *Mirabilis* flowers, when the self pattern arises as a somatic variation from the variegated pattern there is no corresponding change in the Mendelian factors for these patterns. In case of seed-sports from variegated-flowered to red-flowered plants, however, the factors for variegation are affected just as in case of green plants arising from variegated ones and of red-eared maize plants arising from variegated-eared ones. The apparently non-inherited somatic variations of maize plants, noted briefly earlier in this paper, are possibly of the same nature as

the somatic variations in variegated flowers of *Mirabilis*. Some of these variations in maize are self-red cob patches on otherwise variegated cobs, and dark, variegated grains occurring in patches or scattered over light, variegated ears.

General Considerations

The experiments of de Vries, Correns, Hartley, and East and Hayes, as well as the records reported in this paper, all indicate that certain somatic variations are inherited in strictly Mendelian fashion. All these somatic variations consist in the appearance of self-colors on plants that are normally variegated in pattern. The fact that variegated plants occasionally throw both bud-sports and seed-sports with self-colors is not, in general, to be taken as an indication that the variegated plants in question are heterozygous. Such behavior seems to be inseparably associated with variegation. Correns has pointed out (*loc. cit.*) that variegated *Mirabilis* plants can not be considered mosaics of green and "chlorina" types due to heterozygosis, since they do not segregate into chlorina and green, but into variegated and green. The same reasoning applies to variegation in the color of maize ears. Variegated-eared plants do not throw reds and whites, but reds and variegates. The conclusion seems irresistible that self-color occurring as a somatic variation is due to the change of a Mendelian factor for variegation into a factor for self-color. If this be granted, the behavior of these variations in later generations is a mere matter of simple Mendelian inheritance.

From the title of his paper and the tone of his discussion, it is clear that Correns regards, as the most significant feature of these inherited somatic variations, the change from a homozygous to a heterozygous condition. He even refers to them as cases of "vegetativen Bastardierung" or "autohybridization." To me, however, the essential feature is the change of one Mendelian factor into another. The fact that this modification of genetic factors results in a change from homozygosis to heterozy-

gosis seems wholly incidental. It follows from the circumstance that usually only one of the two *V* factors of somatic cells is modified. My own data do not in fact show that the change always affects only one of the factors at a time. While the results prove that this is true in a part of the cases at least, the F_1 ratios suggest the possibility of both factors being modified in some cases.

It is of course utterly impossible at the present time to conceive of the cause or even of the nature of this change in factors from *V* to *S*. We can only conjecture at present as to whether the change may possibly be associated with changing metabolic processes in the maturing plant, or perhaps be connected in some way with changing external influences, or even be a quality inherent in the *V* factor itself. It is perhaps significant that in maize, at least, the change, whatever its cause, occurs very rarely early in the life of the plant and apparently becomes increasingly more frequent as the plant matures. Wholly red ears in variegated-eared plants are extremely rare; large patches of red grains are somewhat less rare; individual red grains occur on most variegated ears; red stripes on the individual grains are very frequent, in fact all but universal in some strains, though in other strains —very light variegated ones—there may be only a few striped grains on a whole ear, the others being wholly colorless. As a matter of fact, even the presence of an ear with red pericarp throughout on a variegated-eared plant may not be good evidence that the change in factors occurred before the ear began to form. If the change took place before the ear was laid down, it would seem that the cob should always be self-red, since the red-eared progeny of such modified grains of the variegated parent plant invariably have red cobs, and cob and pericarp colors are coupled absolutely in later generations. But red ears, or nearly red ears, with light variegated instead of red cobs, have been found to occur as somatic variations on variegated-eared plants. Such behavior suggests that sometimes the factor change may occur almost simul-

taneously in the rudiments of every grain so that the grains become self-red while the cob remains variegated. We might, of course, account for the appearance of self-colored grains on a variegated cob on the basis of separate factors for cob and pericarp color[10] by the assumption that one of these factors may be modified while the other remains unchanged. But we should then have the no less difficult problem of accounting for the universal appearance of red cobs with F_1 red ears without respect to whether the parent grains stood on red or variegated cobs.[11]

Forced to its logical limit, our conception of the *V* factor is that of a sort of temporary inhibitor, an inhibitor that sooner or later loses its power to inhibit color development, a power that once lost is ordinarily never regained. Of course it may be that there is present in variegated maize merely a dominant factor for self-color, *S*, that is temporarily inactive, but that sooner or later becomes permanently active. Even if this be true, *S* as an active factor and *S* as an inactive factor are certainly as distinct in inheritance as they are in development and therefore deserve to be designated separately. And since in one case there results self-color and in the other variegation, the factors may as well be called *S* and *V* as anything else. It is of course also conceivable that the *S* factor may repeatedly arise *de novo,* though this seems very unlikely.

Whatever our conception of the nature of the factors for variegation and for self-color in maize ears, these factors are certainly as distinct in inheritance as any two factors could well be. Moreover, there is abundant evidence, which can not be given here, that they are strictly allelomorphic, as indeed they must necessarily be if one arises by modification of the other—this on the assumption that the factors are definitely localized in certain

[10] Evidence that there are distinct factors for cob and pericarp color was presented in a previous paper on coupling and allelomorphism in maize. Ann. Rpt. Nebr. Agr. Expt. Sta., 24: 59–90. 1911.

[11] This problem is discussed in another paper on the simultaneous modification of distinct Mendelian factors. AMER. NAT., 47: 633–636. 1913.

chromosomes. Furthermore, these factors are to be regarded as *pattern* factors. Though they must influence the development of the pigment in order to produce a pattern at all, they are now known to be distinct in inheritance from the factors for pigment—a fact that I have been able to show by use of a race of maize with a peculiar brown pericarp in addition to races with red pericarp.

Summary

A somatic variation in maize is shown to be inherited in simple Mendelian fashion. The variation has to do with the development of a dark red pigment (or in one stock a brown pigment) in the pericarp of the grains, often associated with the development of an apparently similar pigment in the cob and husks.

Plants in which this pigment has a variegated pattern may show any amount of red pericarp, including wholly self-red ears, large or small patches of self-red grains, scattered self-red grains, grains with a single stripe of red covering from perhaps nine tenths to one tenth of the surface, grains with several prominent stripes and those with a single minute streak, ears with most of the grains prominently striped and ears that are non-colored except for a single partly colored grain, and probably also plants with wholly self-red and others with wholly colorless ears.

It is shown that the amount of pigment developed in the pericarp of variegated seeds bears a definite relation to the development of color in the progeny of such seeds. This relation is not such that seeds showing say nine tenths, one half, or one tenth red will produce or even tend to produce plants whose ears as a whole or whose individual grains are, respectively, nine tenths, one half, or one tenth red. Experimental results indicate rather that the more color in the pericarp of the seeds planted the more likely are they to produce plants with wholly self-red ears, and, correspondingly, the less likely to yield plants with variegated ears.

Self-red ears thus produced are shown to behave in in-

heritance just as if they were hybrids between self-red and variegated races or between self-red and non-red races, the behavior in any given case depending upon whether the parent variegated ears were homozygous or heterozygous for variegated pericarp and whether they were self-pollinated or crossed with white.

It is suggested that these results may be interpreted by the assumption that a genetic factor for variegation, *V*, is changed to a self-color factor, *S*, in a somatic cell. All pericarp cells directly descended from this modified cell will, it is assumed, develop color, and of the gametes arising from such modified cells one half will carry the *S* factor and one half the *V* factor if only one of the two *V* factors of the somatic cells is changed, or all such gametes will carry *S* if both *V* factors are changed.

The *V* factor is thought of as a sort of temporary, recessive inhibitor that sooner or later permanently loses its power to inhibit color development, becoming thereby an *S* factor. Or it may be that the dominant factor, *S*, is temporarily inactive, but sooner or later becomes permanently active. Again, the *S* factor may repeatedly arise *de novo*. The cause of any such change in factors is beyond intelligent discussion at present.

The results of Correns with *Mirabilis* and of de Vries with *Antirrhinum* are shown to be subject to the same analysis as that used to interpret the results secured with maize.

Restoration of *Edaphosaurus cruciger* Cope.

RESTORATION OF EDAPHOSAURUS CRUCIGER COPE

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IN the year 1882 Cope described from the Permian beds of Texas, an imperfect reptilian skull which he called *Edaphosaurus pogonias.* Two years later he described for the first time, the wonderful vertebræ with elongate spines bearing lateral projections on the sides. These vertebræ he assigned to the same genus as the skull but later they were removed to a separate genus as he considered that the two specimens represented different forms of reptilian life. The vertebræ with long spines and cross pieces were placed in the genus *Naosaurus*—"Ship-lizard," a name suggested by the fancied resemblance of the spines with their lateral projections to the masts and yard-arms of a full-rigged ship.

From the time of the original description until 1907 the two genera were regarded as distinct but in that year Case[1] suggested that the two genera should be united and that the skull described as *Edaphosaurus* by Cope belonged with the vertebral column and limb bones described under the name *Naosaurus.* The similar condition of elongate spines, but without cross pieces, on the vertebræ of the carnivorous genus *Dimetrodon* very naturally led to the belief that the two forms *Edaphosaurus* and *Dimetrodon* were similar in other parts of the body and *Naosaurus* merely exhibited something of the extravagance in spines, rugosities, tubercles, etc., which is such a common feature in the most highly specialized members of any group which is approaching the final stages of its family or generic life. The close relationship of the two genera was so probable that it was accepted by all paleon-

[1] Publication 55, Carnegie Institution of Washington.

tologists and even Case was very reticent in his suggestion that they were much farther apart than was usually thought. Following the generally conceived idea of *Naosaurus* a composite mount was prepared in the American Museum of Natural History in New York in which the skull and limb bones of a *Dimetrodon* were associated with the vertebral column of a *Naosaurus*. This restoration was published by Dr. Osborn in the Bulletin of the American Museum and a model of the creature in the flesh was prepared under his direction by Mr. Chas. Knight. Case in his "Revision of the Pelycosauria of North America" republished this restoration by Osborn but at the same time published an alternative restoration in which the skull described as *Edaphosaurus* was associated with the vertebral column of *Naosaurus* and the two genera were united under the former name, as it had priority.

The composite restoration prepared at the American Museum has gained wide circulation in the text books but later discoveries have shown that it was unfortunate. In the summer of 1911 Dr. F. v. Huene, of Tübingen, while a guest of the joint expedition from the universities of Chicago and Michigan to the Permo-Carboniferous beds of New Mexico, discovered the remains of a skeleton of *Edaphosaurus* in which both the skull and a portion of the vertebral column were preserved. As the vertebræ bore the typical cross-pieces of the genus *Naosaurus* the identity of the two genera was established but new evidence was speedily coming; Case in the summer of 1912 discovered in the Permo-Carboniferous beds of Archer County, Texas, the nearly perfect vertebral column of an *Edaphosaurus* (*Naosaurus*) *cruciger* Cope with the limb bones, and a crushed skull, identical with the skull originally described as *Edaphosaurus*.

From this skeleton, now preserved in the museum of the University of Michigan, the author has prepared the restoration shown in Fig. 1. The only conjectural parts are the size of the feet and the length of the tail; the re-

mainder is based upon careful measurements from a single specimen. So far from being a carnivorous, raptorial animal similar to *Dimetrodon, Edaphosaurus* was harmless, molluscivorous or insectivorous with possibly some ability to masticate vegetable matter. The edges of the jaws were lined with sharp conical teeth and upon the palate and the dentary bones were strong plates supporting numerous blunt, conical teeth. The head in all specimens recovered seems rather small for the size of the body and in this is peculiar in the Permo-Carboniferous reptilian fauna, in which the reverse is the rule. The shape of the head in the restoration is taken from the nearly perfect and undistorted skull in the museum of the University of Chicago. The elevated dorsal spines begin with the third vertebræ and speedily reach a considerable height. The lateral projections are elongate at the base of the spine but above the middle are reduced to mere nodules irregularly arranged. The author is not in accord with the suggestion made by Jaekel and Abel that the spines were separate, and can see no reason for the suggestion made by the former that the spines were movable. The strongly interlocking zygapophyses render such an idea impossible to any one familiar with the skeleton. Nor does the author believe that the spines were of any use to the creature as offensive or defensive weapons; rather, as he has frequently expressed himself, he believes that they were in the nature of excessive growths which may have had their inception and impetus in some useful function, but grew beyond that use as the animal became more specialized. The union of the spines into a thin dorsal fin is far more probable and the idea is supported by the presence of rugosities and the channels of small nutrient vessels such as would lie beneath a thick dermal covering. The anterior and posterior faces of the bases of the spines have sharp, low ridges which give place to shallow grooves farther up the spine; only near the top are the spines similar on all sides. Moreover in the living genus *Basiliscus,* which has elevated dorsal spines,

and in the genera of the chameleons in which the same thing occurs, for example, *Chameleo cristatus* Stutch., the spines are united into a thin dorsal crest by the integument and are further united by a thin membrane carrying scattered muscle fibers. The outline of the dorsal fin shown in the restoration is suggested by all the specimens in which the spines have been preserved. The sharp recurvature of the spines in the lumbar region is less pronounced in the specimen from which the restoration was drawn than in some other and it is possible that in other species there was even more of an overhang of the posterior end. The spines are abruptly shortened in the pelvic region and rapidly decrease on the tail. The length of the tail is not known but in all probability was elongate rather than short and stumpy.

The limbs were short and heavy with the forearm and foreleg shorter than the proximal segment of the limb, a condition which is quite common in slow moving forms or those of aquatic or palustrial habit, and just the reverse of the condition found in the active, raptorial *Dimetrodon*. The bones of the feet have not been found in position, but in the great Brier Creek Bone-bed in Archer County, Texas, excavated by an expedition from the University of Michigan in the summer of 1913, numerous large foot bones of a character different from those of *Dimetrodon* or the cotylosaur *Diadectes* were found associated with the spines of *Edaphosaurus* and with large claws. It is believed that the foot of that animal was of goodly size and armed with sharp claws well fitted for digging in the soft earth or vegetation, tearing open rotten logs and overturning rocks in search of food.

It has been noted by all collectors in the Texas beds that isolated vertebræ of *Edaphosaurus* are among the most common fossils found but that any portion of an associated skeleton is extremely rare. This has led to the suggestion that the remains of the animals were transported for some distance after death, probably by rivers from a higher land.

Edaphosaurus was a highly specialized creature, sluggish in movement and entirely harmless, living upon molluscs, insects and perhaps vegetation. It probably lived in the woods or near swamps at some distance from the lowlands upon which were deposited the deltas which make up the Wichita and Clear Fork formations.

In conclusion the author wishes to express his thanks to Dr. Ruthven, of the University of Michigan, for many valuable suggestions in arranging the pose and proportions of the restoration, and to Mr. Irwin Christman, of the American Museum, for the painstaking care with which his suggestions have been followed in making the drawing.[2]

[2] A full account of the known specimens of *Edaphosaurus* and *Naosaurus* and a complete synonymy of the two genera will be found in Publications 55 and 181 of the Carnegie Institution of Washington.

SHORTER ARTICLES AND DISCUSSION

HUMIDITY—A NEGLECTED FACTOR IN ENVIRONMENTAL WORK

An admittedly rough but probably fair estimate of the relative interest which has been taken in the relation of the various environmental factors to insects, at least, may be made from the fact that Bachmetjew in his admirable compilation[1] of the work along these lines devotes, in round numbers, four hundred pages to temperature, one hudred and fifty to food and chemicals, seventy to light, forty-five to humidity, fifteen to electricity and magnetism and thirty to mechanical and other factors. Why is it that temperature is given about a third more attention than all the other factors put together? Is it true that it is nearly ten times as interesting or important as humidity?

A partial answer to the first question undoubtedly is that temperature is easily controlled as well as measured, whereas humidity, for example, is not easily controlled and the means of measuring humidity in small containers are untrustworthy and expensive. Furthermore, work with temperature gives results. The unfortunate part is that these results have usually been ascribed wholly to temperature.

In the course of some work at the Carnegie Station for Experimental Evolution I found that I could change to a surprising extent the markings on the larvæ of a moth (*Isia isabella*) by varying the temperature at which they fed and moulted. However, such changes were much more definite when the temperature was kept constant and humidity varied. I did not have the necessary apparatus for getting accurate control of either factor, but I feel confident that temperature had little or no direct influence. It was acting through its influence upon humidity.

It would seem unnecessary to urge upon experimenters such a fundamental principle in the logic of cause and effect, but the fact is that with only two or three exceptions none of the more than a hundred papers having to do with the effect of temperature upon insects tell us anything about the effect of temperature

1 "Experimentelle Entomologische Studien vom physikalisch-chemischen Standpunkt aus." Zweiter Band. Sophia, 1907.

per se. A few state that the atmosphere was "moist" or "dry," but even then how moist or how dry is not usually mentioned unless it is believed to be saturated or absolutely free from moisture. It is clearly incumbent upon the one who makes such a criticism to show, either by his own work or in a review of that of others, that humidity is a factor of such importance that the criticism is worth the making—especially since the point is so self-evident and has been made in the past. The following notes are an attempt to justify the preceding.

The experiments of many workers show that when lepidopterous pupæ are subjected to abnormal temperature part, at least, of the adults which emerge differ from the normal. The observations have usually been made on color changes, and Fisher[2] especially has shown that warm conditions (36° to 41° C.) produce the same or similar effects as do cold conditions (0° to 10° C.), also that hot conditions (42° to 46° C.) produce effects which are similar to those produced by freezing (—20° to 0° C.). Fisher apparently had no means of successfully controlling the humidity but Tower[3] claims to have had this in his "Investigation of Evolution in Chrysomelid Beetles of the Genus *Leptinotarsa*" and he obtained similar results, stating them as follows:

> The result produced by either a higher or a lower temperature is the development of a greater amount of pigmentation and a consequent melanic tendency in variations. This stimulus in both directions to increased pigmentation reaches a maximum between 5° and 7° C. deviation from normal. Beyond these, as the temperature further deviates, there is a rapid fall in melanism, first to the normal, and then to a condition below normal, until a marked albinic tendency is found; and this decrease in pigmentation continues until the zero point is reached, beyond which no pigment whatever is produced. The zero point is reached much sooner, however, in high-temperature experiments than in low.

Tower then gives the results of experiments in which all the environmental conditions, except humidity, are "normal." Normal humidity for *Leptinotarsa decemlineata* is taken as ranging from 43 per cent. to saturation with an average of 74 per cent. The humidity in various experiments ranges from 10 per cent. to saturation. The lowest natural humidity of which I have seen a record is 5 per cent. It occurred in Death Valley, California,

[2] See *Archiv für Rassen- und Gesellschafts-Biologie*, 1907, IV, pp. 761–793, for Fisher's statement concerning criticisms of his conclusions.

[3] Carnegie Institution of Washington, Publication No. 48, 1906.

where the monthly means for May to September inclusive varied from 20 per cent. to 27 per cent. The annual mean at Cairo, Egypt, is 56 per cent. and at Ghardaia (Algerian Sahara) is 50 per cent. at 7 A.M. and 26 per cent. at 1 P.M. The humidity at Buitenzorg, Java, during the height of the rainy season fluctuates between 70 per cent. and 97 per cent. during the day. Naturally, when dew is being deposited the humidity is practically 100 per cent. It will be seen then that even Tower's extreme averages (see below) are not beyond the range of possibility in nature, although they are as great as it is possible to use in experimental work, since at an average of 34 per cent. humidity only 0.4 per cent. of the larvæ reached the adult stage and atmosphere can not be kept supersaturated.

The beetles were seriated according to an arbitrary scale in which "20 equals total melanism and 0 total albinism." It is difficult to suggest a better method of measuring the extent of melanism than this, although we could wish for diagrams to aid us in grasping just what the scale means. I have tabulated the experiments and interpolated the normal data.

Relative Humidity		Per Cent. of Mortality	Melanism	
Average	Range		Mode	Range
100	100–100	90	4	2–9
95	82–100	30	7	3–11
84	55–100	15	12	7–16
74	*43–100*	*?*	*9*	*5–13*
66	33–100	35	11	6–18
60	30–100	80	5	3–11
50	25–83	92	3	1–7
34	10–55	99.6	2	1–4

It will be seen that mortality increases rapidly as the humidity departs from normal but this can not account for the change in color since the range of melanism is doubled and in three of the experiments even the mode falls below the normal range. As stated by the author:

> The results of experiments with deviations of humidity are almost exactly the same as those which were obtained from experiments with deviations of temperature. Such deviations from the normal either toward an increase or a decrease, produce up to a maximum increased pigmentation and a consequent melanic tendency, but beyond this the effect is reversed, pigmentation is retarded, and the tendency toward albinism becomes more and more pronounced as the deviation from the normal becomes greater.

The point which concerns the present discussion is that not only does humidity have a definite regularly acting influence, but that its results are similar to those of temperature and, as with temperature, plus and minus variations of certain intensities bring about similar effects. If, as has usually happened, the humidity is not controlled in experimental work on the effect of temperature, how can it be said that the observed results are the effect of changes in temperature?

Tower made certain experiments in which both temperature and humidity are abnormal, normal average temperature being taken as 22.2° C. Unfortunately, proof reading or something of the sort was faulty when it came to publication. Experiment 26 would be the most valuable for our present purpose, but the table includes records of relative humidity 35 and 39 per cent. above normal, *i. e.,* relative humidities of 109 and 113 per cent., respectively, if, as in the other experiments, 74 per cent. is "normal" humidity. These are clearly impossible. The text figure illustrating this experiment does not help us since humidities are not given and furthermore the temperatures in the figure are rather consistently one degree different from those given in the table. Since there are two errors in text-figure 15, which illustrates the experiments with humidity as the only variable, it is likely that the figure is the thing that is at fault here. Several other similar discrepancies could be pointed out (as, for example, the temperatures in experiment 24, which concerns the combination effect of humidity and temperature) but it is probable that the author's notebook records are correct and the temperature discrepancies in the published report are so slight that we may accept his conclusion. It is

> that when temperature and moisture are the variables in a given environmental complex, the trend of general color modification is controlled by moisture (relative humidity), excepting in conditions where the temperature deviation is so excessive that the ordinary physiological and developmental processes are greatly inhibited. In experiments approximating natural environmental complexes, however, moisture is the dominant factor in influencing coloration.

Even if there were no other reasons for urging the necessity of taking humidity into account, I feel that Tower's work would be ample justification. Before taking up those reasons let us notice several cases where, on account of the striking results of the experiments, we must regret our lack of information as to the real cause or the relation of the several causes.

This same work of Tower is one of them. The effects just noted were merely ontogenetic. However, he made other experiments in which the effect seemed to be passed on by heredity. The factors in the various experiments with *L. decemlineata* were 35°, 45 per cent. and low atmosphere pressure (p. 287); "hot, dry" (p. 288); "hot, dry and low pressure" (p. 288); and "hot, moist" (p. 291), probably 31.2°, 94 per cent. Those with *L. mulitæniata* were 30° and saturation (p. 292 and p. 293); and the one with *L. undecemlineata* was "10 C. above the average and a relative humidity of 40 per cent." The work is of such importance because of its pioneer character that it would be ungracious to complain too strongly, but the fact is that it is impossible to tell from the data given whether the effects are caused by humidity or by temperature or by a combination of the two. Bateson's idea that there are no effects to be explained need not concern us here.

There is a long series of interesting papers starting in 1895 by Fischer. As has already been mentioned, he finds that certain high temperature grades produce effects which are similar to those produced by certain low temperature grades. The conditions of humidity are rarely mentioned, not to say considered. However, he occasionally confesses that they are important, as when he tells us[4] that it is necessary to have the warm air dry and the cold air moist in order to get similar forms of *Vanessa* by the application of moderate cold and moderate heat. I suspect humidity largely enters into the other experiments also for in one with high temperature,[5] which gave the same results as certain low temperatures and presumably high humidity he says the humidity was high.

Like Tower's experiments with beetles these concern color alone. Pictet[6] and Federley,[7] especially, have considered the effect of environmental factors upon the form of lepidopterous scales. Federley calls his work "Temperatur-experimente" and Pictet "Influence de l'Humidité" but neither enables us to differentiate the effects of the two factors, although both obtained striking results. Kominsky[8] modified to a considerable extent

[4] *Algemeine Zeitschrift für Entomologie,* VIII, p. 274, 1903.

[5] *Illustrierte Zeitschrift für Entomologie,* IV, p. 134, 1899.

[6] *Mémoires de la Société de Physique et d'Histoire Naturelle de Genève,* XXXV, Fasc. 1, 1905.

[7] *Festschrift für Palmen,* No. 16, Helsingfors, 1905.

[8] *Zool. Jahrbücher. Abt. für Allg. Zool. und Physiologie,* pp. 321–338, 1911.

not only the color and form of scales but also the form of antennæ, legs and other body parts of Lepidoptera. He exposed the pupæ to 42.5° C., humidity not given; 38° to 39° C. and 42° to 43° C., relative humidity 80; 8° C., "high humidity"; 0° C., "very high humidity"; —7.5 to 5° C., relative humidity 80–90 and 50; and —11° C., humidity not given. For the most part the humidity was high and probably had much to do with the results, but we can not be certain.

All the experiments just considered were made upon pupæ. It should be remembered that only about one fourth of the weight of lepidopterous pupæ consists of solids, and that the only way they can replace fluids lost by evaporation is by chemical changes in these solids. It is probable that they do so to some extent, although this has not been accurately determined. It is known that under normal conditions pupæ lose in weight and the percentage of solids increases. Naturally, a change in the humidity of the surrounding air would modify this physiological process and it is difficult to believe that it has not quite as much effect as changes in temperature, the humidity remaining the same. It is easy to see that, if the air is made more absorptive or less absorptive either by the temperature changes themselves or by other means, and then the physiological activities are slowed or quickened by temperature changes, the effects will be much greater and might easily pass as due entirely to the temperature changes.

The species which have wet and dry season forms in regions where the temperature is fairly constant throughout the year, as well as the tendency for the animals of moist regions to be melanic and of arid regions to be light colored, speak for the important influence of humidity. But there is another point in distribution to be considered. The study of distribution was long, and still is, largely an effort to get the ranges of animals and plants to fit isotherms. When yearly averages do not work, winter minima or summer maxima or accumulated temperatures are tried. The success which often attends these efforts shows that man is very ingenious and also that temperature is really one of the controlling factors, but it does not show that it is the only factor or, in fact, that it has any direct influence.

The areas of grassland and forest in North America cut across isotherms as though they were merely political boundaries but Transeau[9] has shown that if we plot the ratio of temperature to

[9] Amer. Nat., XXXIX, pp. 875–889, 1905.

humidity we get a very close correspondence between distribution and climatic factors. Schimper[10] has brought together a great deal of evidence which indicates that, as far as plants are concerned, even the major divisions of the world's surface into arctic, temperate and tropical are fundamentally a question of the demand for and supply of water.

Furthermore, if recent climatic changes have an effect upon the origin of new characters and the distribution of the organisms possessing certain characters, humidity is deserving of more attention than temperature, since practically the only evidence we have of such changes concerns humidity.

It should not be forgotten that even aquatic organisms are subject to what amounts to changes in humidity. Peat bog plants take on many characteristics of a desert flora, although their roots are covered with water. It is water, however, which is not easily available, because of the chemicals which it carries. It is water which is physiologically dry.

Finally, the great amount of work which has been done upon artificial parthenogenesis and related subjects is, in a way, a study of the influence of environmental factors. The obvious factors concerned have usually been various chemicals but at foundation humidity, in a broad sense, the addition or withdrawal of water by osmosis seems to be a factor of prime importance.

Frank E. Lutz

American Museum of Natural History

[10] "Plant Geography upon a Physiological Basis," translated by W. R. Fischer. Oxford, 1903.

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A MONTHLY JOURNAL

Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Evolution

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THE EFFECT OF EXTENT OF DISTRIBUTION ON SPECIATION

ASA C. CHANDLER

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While engaged in some research work on the geographic distribution of mammals under the supervision of Professor H. D. Reed at Cornell University in the fall of 1910 and the spring of 1911, certain conceptions regarding the relation between extent of distribution and the generic and specific modifications of mammals were brought to light. Due to the valuable and helpful criticism of Professors C. A. Kofoid and J. C. Merriam, and Dr. J. Grinnell, and of other members of the University of California, and to the advice and aid of Professor C. A. Kofoid, the rather vague ideas then formed have been worked over and crystallized into their form as presented in this paper.

In the past, much of the work that has been done on zoogeography has dealt with a study of the facts of distribution, both present and past, as they stand, together with a study of the factors influencing distribution and speculations regarding the explanation of some of the interesting and apparently anomalous facts thus brought to light. In all of this work, the distribution of animals has been considered almost entirely as the effect of certain biological and geological causes. The present paper is intended to show that the distribution of animals is not only the effect of other causes, but is in itself the cause of other effects, and that extent of distribution has a direct influence on the modification and speciation of the group concerned.

To find out how far-reaching and how potent is this effect, much further study is necessary, not only of the distribution of various groups, but of their classification and systematic relationships as well.

In brief, the effect of extent of distribution on groups of different systematic rank may be stated as follows: As the range of a group of animals, be it genus, family, or order, is extended, the species increase out of proportion to the genera, the genera out of proportion to the families, and the families out of proportion to the orders. In other words, if we assume that in a distributional area of certain extent, there are three genera and six species, in a distributional area of twice that size, there will not be six genera and twelve species, but more probably only four or five genera, and twelve species; *i. e.,* if in the first case the index of modification (a term here used to indicate the average number of species per genus) be two, in the second case it will be greater than two.

As new distributional areas are added, other factors remaining equal, there is a constant increase in number of species and subspecies, going hand in hand with a diminishing rate of increase in genera, the result being a constantly larger index of modification as the area inhabited by a group of animals is extended.

It should be remarked that a unit of area in this connection should be considered a distributional unit, not a geographical unit. In other words, while the addition of one hundred square miles might or might not involve a change in the life of a region, the addition of a new "life zone," "fauna," or association" (see p. 155) would inevitably involve a biotic change, and therefore the addition of one or several of any of these distributional areas should be considered as an addition of a unit, comparable to another unit of similar kind.

Two possible ways of testing this hypothesis present themselves. We may compare the faunas of distributional areas of dissimilar size, or we may compare the specific and generic differentiation found within families occupying areas of different extent. The former method we should expect to work out with a fair degree of accuracy, but the latter involves so many modifying circumstances that even if sufficient data were at hand, it would be difficult to prove anything by it. In the first place there is the difficulty of comparing, in a distributional sense, the areas occupied by different families, since, as pointed out above, the geographic areas do not necessarily coincide at all with distributional areas; in the second place, while it is justifiable to compare the speciation of a family in one region with the speciation of the same family in another region, it is of doubtful value to compare the speciation of one family with that of another in the same or different regions, unless the other factors controlling their speciation be comparable or nearly so. In view of this there are few families which could be advantageously compared with each other as to speciation in relation to extent of distribution, yet in the families which do seem to lend themselves to such a comparison, the evidence all points towards the correctness of the law here proposed.

The bats seem as favorable for such an interfamily comparison as any group of mammals that could be selected, and the table (Table I) of their distribution by

TABLE I

Distribution and Speciation of Families of Chiroptera

Data Derived from Sclater and Sclater (1899)

Family	Distribution	Gen.	Sp.	Index of Mod.
Vespertilionidæ	Cosmopolitan	17	190	11.18
Emballonuridæ	Warm parts of both hemispheres	15	79	5.27
Pteropodidæ	Old World	18	110	6.11
Rhinolophidæ	Old World	6	61	10.16
Nycteridæ	Warm parts of Old World	2	15	7.50
Phyllostomidæ	Neotropical	36	81	2.25

families is significant. One family, the Vespertilionidæ, is cosmopolitan, inhabiting every zoologic region and *every* life zone, and it has 11.18 species per genus, the highest of any family of bats. The Phyllostomidæ, on the other hand, has the narrowest range, occupying only the warm zones of one zoologic region, namely, the neotropic, and has in 36 genera only 81 species, giving 2.25 as the

TABLE II

Distribution and Speciation of Families of Insectivora

Data Derived from Sclater and Sclater (1899)

Family	Distribution	Gen.	Sp.	Index of Mod.
Soricidæ	Palearctic, Ethiopian, Oriental and Nearctic regions, all zones	11	125	11.36
Erinaceidæ	Palearctic, Ethiopian, and Oriental regions	2	16	8.00
Talpidæ	Palearctic and Nearctic regions, temperate zones only	11	25	2.27
Tupaiidæ	Oriental region, warm zones	2	15	7.50
Macroscelidæ	Ethiopian region, warm zones	3	17	5.66
Potamogalidæ	Central Africa and Madagascar, tropical zones	2	3	1.50
Galeopithecidæ	Malay only, forests, tropical zones	1	2	2.00
Chrysochloridæ	South Africa	1	7	7.00
Centetidæ	Madagascar	7	21	3.00
Solenodontidæ	Cuba and Hayti	1	2	2.00

index of modification. The other figures in this table are significant, but the indices of modification in the families Rhinolophidæ and Nycteridæ are abnormally large, and will probably be reduced by subsequent subdivision of genera, or discovery of new forms.

Table II shows the generic and specific differentiation

of the various families of Insectivores, but as some of the families have not been as intensively studied as others, and as the conditions affecting their distribution and speciation are so different in different families, we could hardly expect accurate results, and yet the table clearly shows a tendency for the families having wider ranges to have a higher index of modification, the almost cosmopolitan shrews, for instance, having 11.36 species per genus, and the families with restricted range (Galeopithecidæ, Solenodontidæ, Centetidæ and Potamogalidæ), having only 1 to 3 species per genus. The Talpidæ and Chrysochloridæ do not seem to conform in their speciation to what should be expected.

When the specific and generic subdivisions of all the families of mammals have been worked out more perfectly, and their ranges in a distributional sense, *i. e.,* through life zones, faunas, and associations, are more accurately known, some interesting facts concerning the relation between their indices of modification, and the extent of their ranges, might be brought out.

It is interesting to note that there is a considerable number of conspicuous examples of wide-ranging genera which are remarkably poor in species. Among carnivorous mammals there are many such cases, these animals seeming to be adaptable to an almost unlimited range of environmental conditions without modification, or, in other words, their germ plasm is not stimulated to change by altered conditions of climate or environment. The tiger, for instance, is equally at home in the bleak frozen steppes of Siberia, or in the hot humid jungles of India. The genus *Cynaelurus* is widely distributed over the Ethiopian and Oriental regions, and yet it contains but a single species, with several geographic races. Among birds there are a number of similar examples, the most striking case, perhaps, being *Pandion,* a cosmopolitan genus with but a single species. The same peculiar condition occurs among lower animals, as for instance in the Dinoflagellate genus *Diplopsalis,* which is cosmopolitan

TABLE IIIA

Speciation of Mammals in Various Distributional Areas in California

Data from Grinnell (1913A), (1908), Grinnell and Swarth (1913)

Group	Boreal and Upper Transition Zones					
	San Jac. Mts. (350 Sq. M.)		San Bern. Mts. (550 Sq. M.)		Sierra Range (30,000 Sq. M.)	
	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.
Ungulata	1	1	1	1	2	4
Bovidæ					1	1
Cervidæ	1	1	1	1	1	3
Antilocapridæ						
Rodentia	7	8	10	12	21	57
Sciuridæ	4	4	5	5	6	22
Castoridæ						
Aplodontidæ					1	1
Muridæ	2	3	3	5	7	17
Geomyidæ	1	1	1	1	1	5
Heteromyidæ			1	1	1	2
Zapodidæ					1	2
Erethizontidæ					1	1
Ochotonidæ					1	3
Leporidæ					2	4
Carnivora	6	6	2 (7)	2 (8)	14	21
Felidæ	2	2	(2)	(2)	2	3
Canidæ	1	1	1 (2)	1 (2)	3	6
Mustelidæ	3	3	1	1	7	10
Procyonidæ			(1)	(1)	1	1
Ursidæ			(1)	(2)	1	1
Insectivora	2	2	2	2	4	11
Soricidæ	1	1	1	1	2	7
Talpidæ	1	1	1	1	2	4
Cheiroptera	2	3	2	3	4	7
Phyllostomidæ						
Vespertilionidæ	2	3	2	3	4	7
Molossidæ						
Total	18	20	17 (22)	20 (26)	45	100
Indices of modification	1.11		1.17 (1.81)		2.22	

in warm and temperate seas, and yet is composed of not more than two species. No adequate explanation of these exceptional cases has been offered, and it is probable that their speciation, or lack of it, is due to conditions of their existence or constitution which we do not understand, or do not recognize.

To test the law by comparison of faunas of areas of different extent, a series of tabular comparisons of the faunas of various regions of different size and character was made. In all of these tabulations, care has been taken in the choice of areas for comparison to make them of unequal size from a distributional point of view, and to make them reasonably comparable. An arctic and a tropical region, for example, are not considered reasonably comparable as regards number of genera and species, nor is a region on the outskirts of the range of a group considered comparable with a region near its center of distribution.

Table III shows a comparison of the mammals of various parts of California. The regions compared are as follows: (*A*) the boreal and transition zones of (*a*) the San Jacinto Mountain range, (*b*) the San Bernardino Mountain range, and (*c*) the entire Sierra range, including the Warner and Shasta Mountains to the north, and the San Bernardinos and San Jacintos to the south; (*B*) a comparison of all the zones of (*a*) the San Jacinto Mountains with the immediately adjoining country, (*b*) the Sierra range as defined above, and including their foothills, and (*c*) the entire state.

A careful study of Table III brings out a number of interesting and significant facts, and bears out the law here proposed with unexpected accuracy, barring one seeming exception which, as we shall see later, can not truly be considered as such.

Let us compare first the three areas in which only the two uppermost life zones are involved, and from which the species invading only the lower Transition zone have also been excluded. First, a word as to the areas compared. The Boreal and Transition zones of the Sierras take in over one half of all the representation of these zones within the whole state. These zones of the San Bernardino and San Jacinto mountain masses are, as compared with the entire range, very small indeed, and comprise almost as small areas as could justifiably be

TABLE IIIB

(Data as above)

(Data as in Table IIIA)

Group	All Zones					
	San Jac. Mts. (2,500 Sq. M.)		Sierra Range (60,000 Sq. M.)		California (158,000 Sq. M.)	
	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.
Ungulata	2	2	3	7	4	10
Bovidæ	1	1	1	2	1	2
Cervidæ	1	1	2	5	2	7
Antilocapridæ					1	1
Rodentia	16	41	28	110	31	203
Sciuridæ	5	7	7	26	7	41
Castoridæ					1	2
Aplodontidæ			1	1	1	2
Muridæ	5	14	10	33	11	64
Geomyidæ	1	4	1	9	1	19
Heteromyidæ	3	12	4	24	4	48
Zapodidæ			1	2	1	5
Erethizontidæ			1	1	1	1
Ochotonidæ			1	3	1	3
Leporidæ	2	4	2	11	3	18
Carnivora	9	10	15	29	17	51
Felidæ	2	2	2	3	2	6
Canidæ	3	4	3	9	3	17
Mustelidæ	3	3	7	13	9	22
Procyonidæ	1	1	2	3	2	4
Ursidæ			1	1	1	2
Insectivora	3	3	5	12	6	20
Soricidæ	2	2	3	8	4	14
Talpidæ	1	1	2	4	2	6
Cheiroptera	4	7	7	12	11	26
Phyllostomidæ					1	1
Vespertilionidæ	4	7	6	11	8	21
Molossidæ			1	1	2	4
Total	34	63	58	170	68	310
Indices of modification	1.85		2.93		4.56	

considered to be individual faunal units. The San Jacintos are somewhat smaller than the San Bernardinos, but the difference is almost inconsiderable when compared with the Sierras. Before examining the table, let us see

what conditions in number of genera and species would be expected in these three areas. The San Bernardinos, being almost as small a faunal unit as should be separately considered, we should expect to approach a minimum index of modification, *i. e.*, a minimum number of species per genus, approaching one as a limit. On the San Jacintos, these being smaller than the San Bernardinos, we should expect fewer types according to the law suggested by Grinnell and Swarth (1913), that the number of persistent types in a disconnected area varies directly with the size of the area. On the entire Sierra range we should expect, due to the greatly increased territory, a considerable increase in genera, but a very much greater increase in species. Looking now at Table III, we find that with the single exception of the carnivores on the San Bernardino Mountains, not one discrepancy exists. The Ungulates, Insectivores and bats are represented by the same numbers of genera and species on both of the small areas, and all of them show a marked increase in genera and species on the larger area, in every case with an increase in the index of modification.

The rodents, which show a larger degree of differentiation than any of the other groups, show a very interesting advance in the index of modification as the area is extended. The carnivores, as stated above, show a seeming discrepancy, inasmuch as there are six genera and six species existing on the San Jacintos, and only two genera and two species on the San Bernardinos, whereas, if they conformed with our laws of distribution, we should expect at least six, and possibly seven or eight, species to be found there. On page 35 of Grinnell's "Biota of the San Bernardino Mountains" (1908) we find reference to a number of carnivores now rare or extinct on the San Bernardinos, which undoubtedly have been exterminated by man within the last fifty years. Counting these forms, which it seems to me we are justified in doing, the table bears out the law without a single exception, not only for

the total of mammalian forms, but the totals for each order and for each family.

In comparing the three areas in which all the life zones are involved, the truth of the effect of extended distribution on speciation is still more forcibly impressed upon us. In this case we are comparing areas which are successively larger in size, the San Jacintos, with their foothills and low passes involving the fauna of an area of about 2,500 square miles, the Sierras, about 60,000 square miles, and the whole state of California about 158,000 square miles. The following table, derived from Table III, is very significant in showing the diminishing increase of genera, and the constantly increasing addition of species as the area is enlarged.

Group	Genera			Species			Index of Modification		
	San Jac.	Sier.	Cal.	San Jac.	Sier.	Cal.	San Jac.	Sier.	Cal.
Ungulates.....	2	3	4	2	7	10	1.00	2.33	2.50
Rodents......	16	28	31	41	110	203	2.56	3.93	6.45
Carnivores....	9	15	17	10	29	51	1.11	1.93	3.00
Insectivores...	3	5	6	3	12	20	1.00	2.40	3.33
Cheiroptera...	4	7	11	7	12	26	1.75	1.71	2.36
Totals........	34	58	68	63	170	310	1.85	2.93	4.56

By comparing the upper zones of the San Jacintos with the San Jacintos as a whole, and the upper zones of the Sierras with the Sierras as a whole (see Table III), we find that increasing the life zones has in a lesser degree the same effect as increasing the geographic area regardless of zones; in other words, adding life zones tends to have the same effect on speciation as adding faunas and associations without life zones. The following table (derived from Table III) illustrates this:

Mammals	San Jac. (Upper Zones)	San Jac. (All Zones)	Sierras (Upper Zones)	Sierras (All Zones)
Genera................	18	34	45	58
Species................	20	63	100	170
Index of mod..........	1.11	1.85	2.22	2.93

Another rough test of the hypothesis was made in a comparison of the mammalian faunas of some of our

large continental islands and zoologic regions, the results being shown in Table IV. The data used in this table are

TABLE IV

Speciation of Mammals in Various Continental Islands and Zoologic Regions

Data from Sclater and Sclater (1899)

Group	Africa (11,770,000 Sq. M.)		Australian Region (3,390,000 Sq. M.)		Australia (2,947,000 Sq. M.)		New Guinea (312,000 Sq. M.)		Madagascar (228,000 Sq. M.)	
	Sp.	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.	Gen.
Ungulates...	155	35							1	1
Rodents.....	196	41	69	8			18	5	13	7
Carnivores...	59	22							9	7
Insectivores..	73	8							20	9
Bats........	101	19	83	26			39	16	21	12
Lemurs......	8	3							36	11
Primates....	72	6								
Hyraces.....	14	1								
Elephants...	1	1								
Edentates...	6	2								
Marsupials..			144	36			36	14		
Monotremes.			5	3			3	2		
Totals......	685	128	301	73	169	59	96	37	100	47
Index of modification...	5.35		4.12		2.86		2.59		2.13	

by no means up to date, being taken from the summaries in Sclater and Sclater (1899), but the subsequent additions to the faunas of the places concerned, and the splitting up of genera and species, have probably been approximately proportionate in each of the five areas, and therefore the figures used are sufficiently accurate to be significant. Comparing Africa, the Australian region, Australia, New Guinea and Madagascar, which rank in size in the order given, we find that the indices of modification of their mammalian faunas are as follows: Africa 5.35, Australian region 4.12, Australia 2.86, New Guinea 2.59, and Madagascar 2.13. Certainly these figures are significant.

Comparing the mammalian faunas of the various islands of the Philippine Archipelago (Table V), we find that there is even here some corroboration of our law of

TABLE V

SPECIATION OF MAMMALS IN ISLANDS OF THE PHILIPPINE ARCHIPELAGO

Data from Hollister (1912)

Island	Sq. Miles	Sp.	Gen.	Index of Mod.
Luzon	40,969	72	40	1.80
Mindanao	36,292	61	32	1.90
Samar	5,031	16	13	1.23
Negros	4,881	14	13	1.07
Panay	4,611	10	8	1.25
Palawan	4,027	21	18	1.16
Mindoro	3,851	17	11	1.54
Leyte	2,722	9	8	1.12
Cebu	1,762	8	7	1.14
Bohol	1,441	3	3	1.00
Masbate	1,236	5	4	1.25

speciation. Considering the large element of chance in the animal population of a group of islands of such small size as those of the Philippines, where the various islets are at a varying distance from each other, and their faunas have originated from different sources, the relation between their size and the differentiation of their forms is remarkably regular. In Table V, where the main islands have been listed in order of size, with their numbers of genera and species of mammals, the deer have been excluded entirely, since their generic and specific differentiation is in too chaotic a state to be used. The most striking fact brought out by the table is the lead which the two large islands, Luzon and Mindanao, show, not only in total number of forms, but in index of modification as well. With the possible exception of Mindoro and Palawan, practically none of the smaller islands is supporting as large a variety of mammalian forms as could be expected of it, a fact which might be explained in a number of ways.

In all of the tabulations given, the marine mammals have been entirely excluded since the factors affecting their distribution and speciation are so different from those of terrestrial mammals. In the majority of cases marine mammalian families have a paucity both of genera and species, a circumstance brought about by a number of factors. Generally speaking, large, wide-ranging

forms, or forms which are poor in numbers of individuals, are poor in genera and species, possibly due to the comparative uniformity of their environment, which is usually coincident. Most marine mammals are of these kinds, and their paucity of types is emphasized by the comparative uniformity of their environment, even in the most widespread groups. From a distributional point of view, *i. e.*, taking into account life zones, faunas and associations, a cosmopolitan, oceanic, surface group of animals does not range through as great a variety of ecologic niches and environmental and climatic conditions as does a cosmopolitan terrestrial group.

In order to determine whether the principles of distribution and differentiation here set forth would apply to birds as well as to mammals, a number of series of comparisons was made as with mammals, and with exactly comparable results.

TABLE VI

Speciation of Birds in Various California Areas

Data from Grinnell (1913B), (1908), Willett (1912)

Group	San Bernardino Mts. (2,000 Sq. M.)		Southern California (30,000 Sq. M.)		California (158,000 Sq. M.)	
	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.
Passeres	62	82	79	114	87	197
Picariæ	16	20	19	23	20	38
Striges	3	3	7	7	8	15
Accipitres	5	5	10	14	12	17
Columbæ	1	1	2	2	3	3
Galli	1	1	3	3	6	11
Limicolæ	3	3	4	4	9	10
Grues	1	1	5	6	6	8
Waders	2	2	7	7	8	11
Anseres	2	2	5	5	11	11
Other water birds	1	1	12	14	16	26
Total	97	121	153	199	186	347
Index of mod.	1.25		1.30		1.87	

Table VI gives a comparison of genera and species of resident birds of (*a*) the San Bernardino Mountain region, (*b*) Southern California, and (*c*) California as a whole. Almost without exception, in each individual group of birds there is a reduction in the index of modi-

fication as the area is restricted from California to the Pacific Coast region of Southern California, and finally to the San Bernardino region. The totals reflect the trend in each group. While in the largest area the number of genera is considerably less than double what it is in the smallest, the number of species is more nearly tripled. The Southern California area is intermediate.

TABLE VII

Speciation of Resident Birds in Australia and Tasmania

Data from North (1901–1909)

Group	Australia (2,947,000 Sq. M.)			Tasmania (26,000 Sq. M.)		
	Sp.	Gen.	Fam.	Sp.	Gen.	Fam.
Passeres	304	119	26	53	42	15
Picariæ	29	18	6	7	7	3
Striges	9	2	2	1	1	1
Accipitres	27	17	2	11	9	2
Psittaci	57	14	3	11	9	3
Total	426	170	39	83	68	24
Index of generic mod.		4.35			2.83	
Index of specific mod.	2.30			1.22		

Table VII shows a comparison of the families, genera, and species of resident birds of Australia and Tasmania, from North (1901–1909). Here again, in addition to a very marked diminution of the total number of types in Tasmania as compared with Australia, each group shows a considerable decrease in the ratio of genera to families, namely, from 4.35 in Australia to 2.83 in Tasmania, and of species, to genera going from 2.30 in Australia to 1.22 in Tasmania.

Table VIII is a similar comparison of (*a*) the resident birds of Ireland, from Hartert (1912), (*b*) the resident birds of all the British Isles, from Hartert (1912), (*c*) all the species of the Palaearctic region, the great majority of which are resident in one part or another, from Dresser (1902), (*d*) all the species of Japan, many of which are not resident, from Ogawa (1908), and (*e*) all the species of Kamtschatka, where the majority are resident, from

TABLE VIII

SPECIATION OF BIRDS IN VARIOUS PALEARCTIC REGIONS

Data from Hartert (1912), Dresser (1902), Ogawa (1908) and Stejneger (1885)

Group	Ireland (32,583 Sq. M.)		British Isles (120,900 Sq. M.)		Palearctic Region (19,150,000 Sq. M.)		Japan (147,700 Sq. M.)		Kamtschatka (105,000 Sq. M.)	
	Sp.	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.	Gen.
Passeres	57	35	85	42	610	116	180	64	55	38
Picariæ	4	4	7	7	81	21	34	16	8	5
Striges	2	2	5	4	34	11	14	8	4	3
Accipitres	7	4	12	7	66	21	23	14	15	7
Columbæ	4	2	4	2	29	6	12	6	0	0
Galli	4	4	8	7	76	19	11	5	5	3
Limicolæ	10	9	15	11	97	32	45	21	25	17
Grues	4	4	5	5	34	13	27	9	1	1
Waders	1	1	1	1	31	12	23	12	0	0
Anseres	8	8	16	12	64	24	39	21	28	20
Other water birds	23	14	30	15	129	35	83	28	32	18
Total	124	87	188	113	1,251	310	491	204	183	112
Index of mod.	1.42		1.66		4.00		2.40		1.63	

Stejneger (1885). The increase in index of modification from Ireland to the British Isles, and then to the entire Palaearctic region, is almost exactly what should be expected. The greater number of both genera and species in Japan as compared with Kamtschatka reflects the greater variety of ecologic niches in a warm country as compared with a cold one of comparable size. A comparison of the *resident* species of Japan with the resident species of the British Isles would be of very great interest, but such a list of Japanese birds is not available. The very striking similarity between the speciation of birds in Kamtschatka, and that in the British Isles, both in number of genera and of species, is very remarkable. The interesting manner in which the balance of nature is preserved is shown by the large representation of raptorial birds to parallel the abundance of shore birds and Anseres.

That reptiles and amphibians are influenced in their speciation by their distribution is indicated by Table IX, which shows a comparison of the genera and species of amphibians, lizards, and snakes, in three of the geographic areas defined by Cope (1898).

TABLE IX

Speciation of Amphibia and Reptilia in North American Areas

Data from Cope (1889), (1898)

Group	Lower California District (12,000 Sq. M.)			Western Sub-region (500,000 Sq. M.)			Medicolumbian Region (4,500,000 Sq. M.)		
	Sp.	Gen.	Index of Mod.	Sp.	Gen.	Index of Mod.	Sp.	Gen.	Index of Mod.
Amphibia	4	3	1.25	23	10	2.30	130	28	4.64
Lacertilia	17	13	1.30	28	13	2.15	143	31	4.61
Ophidia	16	12	1.33	20	9	2.22	191	45	4.24

The "Lower California district" consists of only the tip of Lower California; the "Western subregion" embraces the Pacific slope of North America from Northern Mexico, east of the Sierras, to Oregon, where it crosses the Sierras to the Rocky Mountains, including northern Idaho, eastern Montana, and most of British Columbia. The "Medicolumbian region" includes northern and central Mexico, and most of the United States and Canada north to a line drawn diagonally from New England to Alaska, interdigitating on its border with the "Holarctic region."

The almost exactly parallel increase in the indices of modification in the three groups of cold-blooded vertebrates considered, as the area is extended, is quite remarkable. All three groups average from 1.25 to 1.33 species per genus in the smallest area, from 2.15 to 2.30 in the intermediate area, and from 4.24 to 4.64 in the largest area.

As suggested by Professor Kofoid, a factor influencing speciation in such diverse vertebrates as mammals, birds, reptiles, and amphibians, should be very widely applicable to speciation in the entire animal kingdom.

A series of statistics relating to various orders of insects and other invertebrates has been compiled to ascertain whether in these groups as well as in vertebrates, the number of species increases out of proportion to the genera, as the size of the area, in a distributional sense, is enlarged.

TABLE X

SPECIATION OF ELATERIDÆ IN VARIOUS AREAS OF UNEQUAL SIZE

Data from Schwarz (1906)

Region	Sq. Miles	Sp.	Gen.	Index of Mod.
Africa	11,770,000	574	55	10.43
Madagascar	228,000	245	36	6.80
India	1,760,000	438	53	8.26
Borneo	296,700	150	40	3.75
Sumatra	184,000	177	41	4.31
Java	50,000	125	35	3.37
Ceylon	25,333	96	28	3.42
Australia	2,947,000	386	42	9.19
New Guinea	312,000	61	20	3.05
New Zealand	104,750	137	.24	5.70
Tasmania	26,000	13	7	1.86

Table X was compiled to show the number of genera and species of beetles of the family Elateridæ in various continents and islands, the regions chosen for comparison being well defined areas of unequal size.

A careful inspection of this table shows that with only two exceptions the indices of modification are directly proportional to the size of the areas. Borneo and New Guinea, however, not only show a smaller index of modification than should be expected of them, but are poor in total number of types. Nevertheless, when we reflect that these two islands are not nearly so thoroughly known to science as are the other areas considered in the table, no great significance can be attached to their seeming paucity of known types.

Table XI shows the number of genera and species of Limnophilidæ, a family of Trichoptera, in eastern North America (east of the Rockies) as compared with North America as a whole. It will be noticed that while in the

TABLE XI

SPECIATION OF LIMNOPHILIDÆ (TRICHOPTERA) IN NORTH AMERICA

Data from Ulmer (1907)

Region	Sq. Miles	Sp.	Gen.	Index of Mod.
North America	8,000,000	98	27	3.63
Eastern North America	5,000,000	45	20	2.25

larger area the number of species is more than double what it is in the smaller area, the increase in genera is only about one third, increasing the index of modification from 2.25 to 3.63.

Table XII shows practically the same thing in the case of the hawk moths of the family Sphingidæ.

TABLE XII

SPECIATION OF SPHINGIDÆ IN AMERICAN AND AFRICAN AREAS

Data from de Rothschild and Jordan (1907)

Area	Sq. Miles	Sp.	Gen.	Index of Mod.
West Indies	76,000	61	20	3.05
Mexico and Central America	975,200	122	34	3.58
South America	7,000,000	197	35	5.62
Mex., Cent. Am., and S. Am.	7,975,200	237	40	5.92
Mex., Cent. Am., S. Am., and W. I.	8,051,200	262	41	6.39
Bourbon	965	7	5	1.40
Madagascar	228,000	39	20	1.95
Africa	11,772,000	166	48	3.45
Africa and Mad.	12,000,000	195	53	3.67
Africa, Mad., and Bourbon	12,000,965	197	53	3.71

In this case two series of tabulations were made, one showing the number of genera and species in various Neotropical areas, and combinations of these areas, the other showing a similar tabulation for various Ethiopian areas, with similar combinations. It will be observed that the speciation in the West Indies is very large for the size of the area involved, but when we consider the abundant opportunity that has been given for isolation to operate, this is not surprising. The index of modification is quite low. Mexico and Central America have a larger speciation, compared with South America, than would normally be expected, the reason being that Central America is the American center of distribution. The index of modification, however, reflects the smaller size of the area, being considerably lower than that for South America. The increase in index of modification from 5.62 to 6.39, as areas are successively added to South America, is significant. Looking now at the Ethiopian regions, we find that there is the same disproportionate increase of species over

genera in successively larger areas, the index of modification increasing from 1.40 in the small island of Bourbon to 1.95 in Madagascar, and 3.45 in Africa. Combining Africa and Madagascar, this is increased to 3.67, and with the island of Bourbon, to 3.71.

Table XIII is one of especial interest, since it deals

TABLE XIII

SPECIATION OF MARINE GAMMARIDEA (AMPHIPODA) IN VARIOUS SEAS

Data from Stebbing (1906)

Area	Sp.	Gen.	Index of Mod.
Mediterranean Sea	147	67	2.19
Arctic Ocean	311	140	2.22
N. Atlantic Ocean	475	176	2.70
S. Atlantic Ocean	65	44	1.47
Arctic and N. Atlantic	588	191	3.07
Arctic, N. Atlantic, and S. Atlantic	645	207	3.11
Arctic, N. Atlantic, S. Atlantic and Med. Sea	735	214	3.43
Whole family	1,333	313	4.22

with a marine instead of a terrestrial group. It embodies the results of a compilation of the marine genera and species of Amphipoda of the suborder Gammaridea in a number of the oceans and seas of the world. Since it is primarily a cold-loving group, the largest numbers are found in the cold seas, the Arctic and North Atlantic being the home of considerably over half of the known marine species. It is very likely that when the Antarctic regions have been studied as thoroughly as the northern regions, the number of species from that part of the world will be very considerably increased. At the time of Stebbing's work on Amphipoda, our knowledge of Antarctic and contiguous areas was very meager.

The steady increase of the index of modification from the smaller to the larger seas is striking. The Mediterranean Sea, although it is the most thoroughly known of all, has the lowest index of modification, namely 2.19, the Arctic Ocean comes next with 2.22, and then the North Atlantic with 2.70. The small number of species from the South Atlantic and Antarctic regions has already been

mentioned, and its low index of modification may be attributed to the same sort of imperfect knowledge as in the case of Borneo and New Guinea in Table X. The constant growth of the number of species per genus from 2.22 to 3.43 as the various seas and oceans are added together, exactly parallels the results obtained in a similar way for a terrestrial group in Table XII. The comparison of the speciation of the largest area for which it was worked out, with the speciation of the entire group, many species and genera of which inhabit fresh water, is interesting, jumping as it does from 3.43 to 4.22. From the facts brought to light by this table it can hardly be doubted that practically the same influence is brought to bear on the speciation of marine as on terrestrial organisms by the extent of their distribution.

The theoretical explanation here proposed for this phenomenon involves a number of complex problems relating to evolution and speciation, including isolation, effect of time, causes of specific and generic modification, etc., each of which will be dealt with in the following pages as they seem to influence the law here proposed.

Let us first consider the factor of isolation in relation to the production of new forms. As excellently stated by Cook (1909), isolation can not be considered as a cause or factor in evolution, since changes in the characters of species are not dependent upon the subdivision of species to form additional species. To quote from him:

> The separation of species into two or more parts allows the parts to become different, but there is every reason to believe that evolutionary changes of the same kind would take place if the species were not divided. That the isolated groups become different, does not indicate that isolation assists in the process of change. It gives the contrary indication that changes are restricted by isolation. If isolation did not confine the new characters to the group in which they arise, the groups would remain alike, instead of becoming different. . . . Isolation is the shears that splits the species, not the loom that weaves it.

Therefore, while isolation can not be considered a factor in evolution, it is an important factor in speciation. Species vary in many directions or orthogenetically pro-

gress in a definite direction, but the trend of variation or progression may be different in one locality, and tend towards a different result, from that of another locality. Whether the evolution, usually in more or less divergent directions, of segregated groups of individuals be looked upon (1) as the accumulation of numerous slight variations which have a different average character in any two portions of a species, as originally explained by Darwin (1859, Chap. 4) or (2) purely as the result of natural selection, as argued by Wallace (1858), or (3) as the result of a change in the average character of two portions due to the uneven occurrence of mutations in the two portions, a conclusion reached by Dewar and Finn (1909, p. 380), or (4) as the result of orthogenetic evolutionary tendencies inherent in the species and influenced by the environment, as Eimer suggested (1897, Chap. 1), does not concern us here,—the general tendency appears to be that two isolated portions of a species as a general rule trend in different directions, and diverge farther and farther as long as they are isolated.

It is assumed that the greater the length of time given for the influence of isolation to be felt, the farther apart are the two originally identical divisions likely to trend, however the dissimilar evolution be interpreted. As stated by Tower (1906), in speaking of the method of evolution of the Chrysomelid genus *Leptinotarsa*,

> We can interpret the conditions found by any of the current hypotheses; but explaining a condition by an hypothesis is not the same as that the conditions found are evidence in support of an hypothesis, although it is often so used.

The existence of distinct variations, subspecies, and ultimately species and genera, in isolated areas is a too frequently observed phenomenon to be looked upon as anything else than a self-evident truth, but that this should necessarily be considered as supporting any particular theory of evolution can not be argued.

The profound results of prolonged isolation may be observed in the fauna of some of our long-separated con-

tinental islands, such as Madagascar, Australia and New Zealand. Decreasing degrees of isolation may be observed in our West Indian islands, where some generic differentiation has occurred; in the Santa Barbara islands, where there has been a differentiation of species; and the detached mountain ranges of Southern California, where the upper life zones are at present in an isolated condition, but have been so only long enough to develop a few new subspecies, and to lose many of the types of the mother range, in accordance with the law proposed by Grinnell and Swarth (1913) that "the smaller the disconnected area of a given zone, or distributional area of any other rank, the fewer the types which are persistent therein."

From this it is apparent that the time element, in conjunction with isolation, may have a very decided effect on the number of genera and species in a family, but since, from a geologic point of view, animals appear to have reached a new equilibrium very quickly after a geographic change, the time element may have little effect on the numbers of genera and species relative to each other in any given area. In other words, as fast as new genera are produced in a given area, the species within the genera will tend to be produced in the same ratio, thus leaving the index of modification unaffected.

As an example of the effect of time and isolation let us take a hypothetical case. Let us assume that a certain island became divided into two islands of unequal size, and that after a short period of segregation, just long enough for the fauna to readjust itself to the smaller areas and reach a new equilibrium, we had say six species in three genera on the larger island, and three of the same species in two of the genera on the smaller one. After a long period of isolation we should have approximately the same number of genera and species on the two islands, but they would have diverged to generic differentiation. In other words, the effect of time in conjunction with isolation is to increase the number of genera and species in the family, while the index of modification undergoes little change.

This leads us to a consideration of the factors involved in the differentiation of genera as contrasted with the differentiation of species. In general it may be said that extrinsic modifications, *i. e.,* those which are in some way connected with changes in temperature, humidity, character of flora, food, and other environmental conditions, and which usually affect such characters as color, size, length of hair, etc., lead to differentiation of species and subspecies primarily. On the other hand, intrinsic modifications, *i. e.,* those which are related directly or indirectly to a change in the habits or mode of life of the animal or the occupation of a new niche in nature, usually, if not always, lead to generic or family differentiation, since it is evident that changes fitting an animal to live arboreally instead of terrestrially, for instance, are of such a nature, that if they are perpetuated and carried to perfection, will not stop at specific difference but will become of generic importance.

It might be argued that there are no modifications which might not, if carried far enough, ultimately lead to generic differentiation. This is possible, but very improbable, because the modifications here alluded to as "extrinsic" are of such a nature that in the varying climatic conditions there are likely to be intermediate forms which make the division of the more widely separated ones into genera impracticable. In the case of our "intrinsic" modifications, intermediate forms are not so likely to exist when once the incipient changes leading to an altered mode of life have reached a fair degree of perfection.

As a concrete example of what is meant by extrinsic and intrinsic modifications, let us take the squirrels of a given region, say eastern North America. There are four genera to be distinguished,—*Sciurius, Tamias, Sciuropterus* and *Arctomys.* The genus *Sciurus* contains strictly arboreal, mostly nut-eating, omnivorous forms. *Tamias* includes forms which are terrestrial, diurnal, dwelling in natural or artificial holes and crevices, and with a device for carrying food in their cheeks. *Sciuro-*

pterus is an arboreal type which is nocturnal, and has developed characters which enable it more easily to travel from tree to tree. *Arctomys* is the most highly modified form, and has departed most widely in its habits; it is entirely terrestrial, seeks shelter in artificial burrows, eats grass, and hibernates.

Were we to study the characters separating these genera, we should find that they are all characters which enable the animal best to occupy the ecologic niche it fills. If now we select any one of these genera and examine its species, we perceive that the differences we find are not such as could clearly be related to differences in mode of life or habits, but rather such differences as are induced by the circumstances mentioned above, such differences being size, color, length of feet and tail, texture of fur, etc.—*i. e.,* extrinsic variations.

An interesting example of both extrinsic and intrinsic modifications in an incipient stage may be found in the song-sparrows of western United States. Let us compare the form of the humid northwest coast belt, *Melospiza melodia morphna,* with the form of the arid Arizona deserts, *M. m. fallax.* The differences to be observed in color and size are very noticeable, and would undoubtedly lead to their separation into two distinct species were it not for the complete chain of intermediate forms. But even if the chain of intermediate forms were not complete, and after a period of segregation the numerous intergrading subspecies became broken up into a few well-marked species, nevertheless, unless a change in mode of life of the bird were involved, however far the extremes of color and size might tend, they could not be given generic distinction because of the intermediate forms, inhabiting semi-arid or semi-humid regions, which would be almost certain to exist. It hapens, however, that *Melospiza melodia morphna,* and *M. m. fallax,* do differ considerably in mode of life, the former being a beach comber, the latter a nomad of the desert. It would be expected, therefore, that if these two subspecies were isolated, the modifications re-

lated to their difference in mode of life, already shown in an incipient manner, would soon lead to their generic differentiation.

It is not argued that under a given set of ecologic conditions, only one type could be produced, nor that according to the idea of some zoologists, as set forth and refuted by Grinnell and Swarth (1913), should individuals of one geographic race be transplanted into the region of a different geographic race, the first race would assume within a few generations all the characters of the second race. Whether the changes due to the influence of the environment be looked upon as the results of natural selection and adaptation, or merely as the results of a stimulus to the germ plasm, the new type would not necessarily be always the same, this, however, depending upon the number of potential responses in the type, and, as excellently shown by Ruthven (1909) in his study of evolution in the genus *Thamnophis*, upon the modifications previously undergone by the type we are dealing with.

It is very evident that there are many variations in animals which seem to fall into neither the extrinsic nor intrinsic category, but which are neutral and vary independently of climate or habits, and may be inherited phylogenetic tendencies. It is very largely due to these neutral variations, frequently to be ascribed to orthogenetic evolution, tending in different directions in different places, and given an opportunity to diverge by isolation, that different species may be produced to occupy regions of similar climatic and environmental conditions, and different genera may be found occupying the same ecologic niches.

To choose an example in the same family quoted before, we may cite the case of *Tamias* in eastern North America, and *Eutamias* in western North America. In this case the characters separating the genera are not clearly related to their mode of life, the chief difference being the loss of one small premolar in *Tamias*, and its retention in *Eutamias*. The extent of divergence of these neutral varia-

tions depends on the duration of *geographic* segregation, and may therefore be of specific, generic, family, or ordinal rank.

To sum up, specific modifications may be of three kinds: (1) extrinsic modifications, induced by changes of climate and environmental conditions; (2) neutral modifications, due to a different trend of evolution in segregated regions; (3) incipient generic modifications. On the other hand, generic modification may be either intrinsic modifications, concomitant with changes in mode of life or habits of the animal, or neutral modifications as above, given generic value by a longer period of segregation.

Having dwelt for some length on these preliminary considerations, let us now apply them to the case in hand and see how they affect differentiation into species and genera through extension of range.

It is a well-known biological fact that different types of a group of animals, at least of higher animals, are found associated with different environments; nearly related species do not, as a rule, live comfortably together in the same environment, and nearly related genera do not occupy the same ecologic niche in a given zoogeographical area. This does not seem to hold true for animals of lower organization, as conclusively shown by Kofoid (1907). It is common for a group of animals, unless hindered by an impassable barrier or unfavorable environmental conditions, not only to continually extend its range into new territory, but also to attempt to live in as many different niches in nature as possible within a given area. Such attempts to invade new ecologic niches are frequently concomitant with heritable modifications better fitting them to occupy their new situation, though it is difficult to say whether these modifications are causes or results of the change in mode of life. However this may be looked upon, the tendency to occupy new niches in nature is frequently accompanied by intrinsic modifications, and therefore by generic differentiation.

From this we may safely assume that in a given area

a family of animals, by adaptive evolution, will approach a maximum of generic differentiation which can be supported in that area. In other words, every suitable ecologic niche which is represented in the region considered will be invaded by the family, and even in a small area there is likely to be a considerable generic differentiation, especially if isolation has had any opportunity to operate within the area, in breaking up the genera and species.

Let us assume that in one unit of area a certain family, Sciuridae for example, was represented by three genera, each with three species. Second, let us assume that this family kept spreading into additional units of area. With each new unit, the chance of new suitable ecologic niches being represented would decrease, and therefore the chance of new genera being represented would decrease, since if a genus were fitted for its niche in nature under certain conditions of climate and environment, it would in the majority of cases not be likely to undergo any radical changes in the occupation of the same niche under somewhat altered conditions of climate and environment; *i. e.,* the stimulus for intrinsic modification would be lacking.

On the other hand, with each additional unit of area, the chances of the combined conditions of temperature, humidity, and environment being different, would remain the same. In other words, the chances of the three dimensions influencing the life of a region, *i. e.,* "life zone" (controlled by temperature), "fauna" (controlled by humidity), and "association" (controlled by the effect of the other two plus a number of other environmental conditions), intersecting at the same point would be almost equally improbable with each succeeding unit of area. Since it is changes in "life zone," "fauna," or "association" which produce extrinsic changes, and therefore lead to differentiation of species and subspecies primarily, the increment of species would average nearly the same for each succeeding unit of area, other factors remaining equal. It should also be taken into consideration that

with the invasion of new zoogeographic areas, contact with allied forms is frequently experienced, and opportunity is thus afforded for cross breeding and hybridization, the result of which upon the germ plasm appears to be as influential in the production of new forms as is the shock of new environmental conditions. The constant increase in species and subspecies accompanying invasion of new territory, going hand in hand with a diminishing increase in genera, results in the constantly larger index of modification as the area inhabited by a group is extended.

SUMMARY

1. Extent of distribution has a direct influence on the speciation of the group concerned in this way, that as the range of a group of animals is extended, the species increase out of proportion to the genera, the genera out of proportion to the famliies, and the families out of proportion to the orders.

2. Comparison of different families having unequal geographic ranges is usually inaccurate due to the great differences in the other factors controlling their speciation. Those families which do lend themselves to such a comparison show decidedly the effect of extent of distribution, *e. g.*, the bats and some of the insectivores, the families of widest distribution having the largest indices of modification. A number of exceptions exist in the form of certain wide ranging genera which have a paucity of species. We have no adequate explanation for this phenomenon.

3. Comparison of the faunas of areas of different size gives very accurate results. A number of tabulations show as a whole an invariable increase in the index of modification as the distributional area is extended by the addition of either life zones, faunas, or associations. Such tabular comparisons were made for all the classes of terrestrial vertebrates, for several families of insects, and for the marine Amphipoda of the suborder Gammaridea. Allowing for explicable exceptions, the increase in number

of lower systematic groups out of proportion to the increase of higher systematic groups as the area considered is enlarged is a remarkably constant and wide-spread phenomenon.

4. The theoretical explanation here proposed for this phenomenon involves a number of complex problems relating to evolution and speciation, including isolation, the time element, and causes of specific and generic modification.

5. Isolation is an important factor in speciation, since the separation of species into two or more parts allows the parts to become different. The degree of divergence of the segregated parts is largely dependent upon the duration of segregation.

6. Time, in conjunction with isolation and evolution, tends to increase the number of genera and species in a family, but the index of modification, *i. e.*, the average number of species per genus, remains approximately the same in a given area.

7. Three types of modifications in animals may be named:—first, "extrinsic" modifications, which are induced by climate and other environmental conditions, and which lead to differentiation of species and subspecies primarily; second, "intrinsic" modifications, which are concomitant with a change in habits or mode of life of the animal, due to the occupation of a new ecologic niche, and which usually lead to generic or family differentiation; and third, neutral modifications, which are merely the result of the natural tendency of all animals to vary and to be subject to more or less orthogenetic evolution,—modifications which can not be correlated with environmental conditions, nor with a change in mode of life of the animal, but which may be influenced largely by inherited tendencies. Such modifications are responsible for the production, through isolation, of different species to live under the same climatic and environmental conditions, and of different genera to occupy the same ecologic niche.

8. Specific modifications may be of three kinds: (1) ex-

trinsic modifications, (2) neutral variations in segregated regions, (3) incipient generic modifications. Generic modifications may be (1) intrinsic modifications, or (2) neutral varations, given generic value by a longer period of segregation.

9. Since different types of a group of animals are usually found associated with different environmental conditions or different ecologic niches, and since it is common for animals, if unhindered, not only to extend their range continually into new territory, but also to occupy new ecologic niches, and since these tendencies lead to specific and generic differentiations, respectively, any given area will have a differentiation of species proportionate to its variety of environmental conditions, and of genera proportionate to its variety of suitable ecologic niches.

10. Since, as the area of distribution is extended, the chance of new conditions of climate and environment being represented remains approximately the same, the increase in number of species is nearly proportional to the increase in the area of distribution, but since the chance of new ecologic niches being represented in most cases constantly decreases, the increase in genera proceeds at an ever-diminishing rate. This, going hand in hand with the nearly constant increase in species or subspecies, results in a constantly increasing index of modification.

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BIOLOGY OF THE THYSANOPTERA[1]

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I. FACTORS GOVERNING LOCAL DISTRIBUTION

Introduction

The Thysanoptera, commonly called thrips, are only beginning to be known, in this country, by systematic entomologists. The systematic knowledge is mostly contained in the monograph of Hinds (1902), a more recent synopsis by Moulton (1911), and a few other papers dealing with new species and with relationships, prominent among which is the work of Jones (1912). Biologically the group is still less known. A considerable number of papers have been issued from experiment stations, describing the life history (egg, larval, pupal and adult stages) and habits of thrips of economic importance. Besides these the principal recent work of a biological nature is a paper of my own (Shull, 1911), on the ecology, method of locomotion, mode of reproduction, and dissemination. The life cycle of most species is still largely unknown.

The first section of this paper is an attempt to carry into further detail the study of the ecology of the Thysanoptera. The first ecological scheme, so far as I am aware, worked out for the Thysanoptera was that of Jordan (1888), who divided thrips into three classes: first, the flower-dwellers; second, the leaf-dwellers; and third, all other thrips (for example, those living on fungi, under wet leaves, under bark of trees, on roots, on lichens, etc.). The inadequacy of this classification, and the difficulty of applying schemes of ecology adapted to other groups of insects, was pointed out in my earlier paper, where I pro-

[1] Contributions from the Zoological Laboratory of the University of Michigan, No. 142 (Biological Station Series, Zoological Publication, No. 10).

posed a new scheme, based on my observations in the field. In this scheme, Thysanoptera were divided into two groups: (1) interstitial species, those living in closely concealed situations, as among the florets of composite flowers, or in clusters of young leaves; and (2) superficial species, those living on exposed surfaces, for example, the surface of leaves. The interstitial species were further divided into an anthophilous division (flower-dwellers) and a phlœophilous division (those living under bark scales on trees). The superficial species were either poephilous (on grass) or phyllophilous (on leaves of plants other than grasses). The distinction between poephilous and phyllophilous seemed warranted, since grass-dwellers were found on many different grasses, but rarely on other kinds of leaves.

Such a classification undoubtedly describes the facts, but does not explain why the habitats named are the ones chosen(?). The factors determining habitat were believed by me at that time to be character of food, and protection afforded. In some species one of these factors predominated, in other species the other factor, while others may have been influenced largely by both. In the light of recent ecological studies, however, the explanation of local distribution in terms of such general environmental factors seems inadequate. Largely owing to the work of Shelford (1911) upon the tiger-beetles, much emphasis is now being placed upon the ecological importance of physiological factors. With a view to relating the distribution of Thysanoptera to the physiology (more specificially, behavior) of the various species, and thus explaining that distribution in more definite terms, the experiments and observations recorded in this paper were made.

This work was done largely at the University of Michigan Biological Station, at Douglas Lake, Michigan, supplemented by observations at Ann Arbor, Michigan, in Ohio and elsewhere.

Facts to be Explained

The following are some of the facts of habits and distribution of the more abundant species for which physiological explanations were sought. Some of these facts are stated in my former paper, some of them doubtless the common property of all thysanopterists; others, so far as I know, have never been recorded.

Euthrips tritici is found almost exclusively *in situations where it is concealed,* as among the florets of composite flowers, in clusters of young leaves, or in almost any close crevice where the tissues are not too hard or tough to be pierced. It appears to make little difference what species of plant is inhabited, provided a concealed situation is available. In the paper cited above (Shull, 1911) I gave a list of seventy species of plant on which *Euthrips tritici* was taken, and I have since collected it on a number of plants not included in that list. But with rare exceptions, it has been found in crevices where it was not readily visible. In related plants, it is always more abundant in those affording concealed situations. Thus, in white clover (*Trifolium repens*) and in red clover (*T. pratense*), this thrips is usually abundant; while on the related yellow, and white, sweet clovers (*Melilotus officinalis* and *M. alba,* respectively), growing along with the red and white clovers, *Euthrips tritici* is usually rare or wanting. The flowers of *Melilotus* are widely separated from one another on the stem, and do not afford concealment (Shull, 1911).

If, while *Euthrips* is in one of these crevices, it is disturbed, as by gently rubbing or pressing the flower, it quickly *comes out of its retreat and crawls rapidly away, or takes to flight.* The larvæ show the same behavior as the adults in this regard, except, of course, that they do not fly.

Anaphothrips striatus is found *usually on grasses* of various kinds, rarely on leaves of other plants. The species of grass seems to make little difference. *Some individuals are found in perfectly exposed situations,* as on

the upper side of grass blades, *others more or less concealed* in the rolled up young leaves (Shull, 1911). I have found, however, that among the adults, *those in exposed situations are almost exclusively females, while those in the rolled young leaves are either males or females.* (For the first time on record, the males of this species, as will be shown in the second part of this paper, have been found in considerable numbers.) The larvæ, according to my observations, *may be either exposed or concealed;* the exposed ones are predominantly the older larvæ.

In one of the grasses (*Spartina michauxiana*) on which *Anaphothrips* was found in abundance at Douglas Lake, Michigan, the leaves bear on the upper surface a set of fine, but prominent, ridges running parallel to the axis of the leaf. Adult females and larvæ of *Anaphothrips* on the exposed parts of these leaves were always lodged between the tops of these ridges, and almost invariably *with their heads toward the base of the leaf.* If disturbed, they began to crawl along the crest of one of these ridges toward the base of the leaf. It was possible to force them to turn in the opposite direction, but if allowed to do so they soon turned again toward the base of the leaf, often continuing until they were among the rolled young leaves in the center of the top of the plant.

Anthothrips verbasci is found exclusively on one species of plant, the common mullein (*Verbascum thapsus*). Furthermore, it is rare that a specimen of mullein, of considerable size, is found free from the mullein thrips. Most of the thrips are found *among the florets or seed pods of the spike.* Less commonly they are to be seen on exposed surfaces, as on the leaves or stem lower on the plant; but *these exposed individuals are mostly adults.* The larvæ are usually hidden on the flower spike unless that situation is crowded by a large number of larvæ; and *the larvæ that are occasionally found exposed are mostly nearly fully grown.*

Anthothrips niger was not abundant enough during my stay at Douglas Lake that many observations of its

habitat and behavior could be made. One fact, however, is of interest in connection with an experiment to be described. While the adults live mostly on flowers, sometimes concealed, sometimes more or less exposed, the larvæ were always found concealed; moreover, *it was with difficulty that the larvæ could be driven from their retreat by pressing the flowers.* Frequently such vigorous squeezing was necessary to dislodge them that the larvæ emerging were injured; and a flower so treated was often found later to contain numerous dead larvæ. In this respect, the behavior of this species is in considerable contrast to that, for example, of *Euthrips tritici.*

The habitats and behavior described above can be "explained" in large measure if we say, as I at first proposed (1911), that certain species seek protection, or that certain other species have specific food requirements. Thus, it might be said that *Euthrips tritici* seeks safety in crevices, and flees danger when disturbed; that *Anaphothrips striatus* "prefers" grass for food, that it requires as much protection as its commissarial activities permit, and that its habitat and behavior are such as best fulfill these requirements. *Anthothrips verbasci* might be said to be limited to one article of diet, while protection is a minor matter.

This explanation might be acceptable as far as it goes, were it not that no species is immune to attack. I have seen larvæ of *Anthothrips verbasci* frequently captured by various bugs. Heads of mullein where thrips are found nearly always bear bugs of the family Capsidæ, and observations convince me that they prey almost wholly on the larvæ of the mullein thrips. The degree to which they check the thrips was tested experimentally as follows: Two mullein spikes of approximately equal size and equally infected with thrips were selected. The predatory bugs were removed from one of them, after which the spike was enclosed in a thin muslin bag. Two weeks later the bag was removed. The enclosed spike bore a large number of full-grown larvæ, a few had

pupated, and many were crawling on the inside of the bag. The spike that was exposed, on the other hand, bore but little over half the number of larvæ that were on the protected one, none were quite full grown, and none had pupated. Since nothing in the climatic conditions (heavy rains, for example) could have caused this difference, it is to be inferred that predatory bugs had devoured the larger larvæ in considerable numbers.

Yet *Anthothrips verbasci,* according to my earlier explanation, "chooses" its habitat almost exclusively in relation to food, protection being a minor consideration.

Can we not explain habitat and behavior in these insects in some way not implying choice, especially choice between conflicting preferences? May we not assume that certain elements of behavior are what they are without reference to their usefulness? If we grant the possibility of an affirmative answer to these questions, the experiments about to be described will have significance.

EXPERIMENTS ON BEHAVIOR

The following experiments were designed to show the reaction of the commoner species of Thysanoptera to what seemed to me the most probable external agents affecting their distribution and behavior, namely, light, contact and gravity. Inasmuch as I was not primarily interested in *how* a given reaction was brought about, but only in its end result, the experiments were rather crude. Refinements were unnecessary, and their omission enabled me to use much greater numbers of individuals than would otherwise have been possible. From ten to forty repetitions of each test were usually made. The experiments are described by species, only representative experiments being given.

Euthrips tritici

Light. Exp. 1.—Adults of this species were placed in a glass tube about three feet long and one inch in diameter, closed at the ends with corks. One end of the tube

was turned toward a small window, while the room was rather dimly lighted. All the thrips crawled rapidly toward the window. When the position of the tube was reversed, the thrips reversed their crawling, again going toward the window. The reaction was definite and invariable.

Exp. 3.—A close-fitting sleeve of black building paper was slipped over one half of the glass tube used in experiment 1. The thrips were collected at the exposed end by turning that end for a few minutes toward the window. The covered end of the tube was then turned toward the window. The thrips crawled rapidly toward the light, until they reached the shadow of the sleeve. Here they crawled about, apparently aimlessly, for half an hour an inch or two within the sleeve or just outside it.

Contact. Exp. 1.—When, in the light experiments, the tube was reversed in position as soon as the thrips reached one end, the insects immediately turned toward the opposite end. But if the tube was allowed to rest for some time, the thrips became settled quietly between the glass and the sloping surface of the cork. The tube could then be carefully reversed, and most of the thrips remained lodged between cork and glass for many minutes, some of them for hours. *The positive reaction to contact counteracted the positive reaction to light.*

Exp. 25.—A larva of this species was placed on a glass plate, upon which rested a microscope slide. When the larva in its crawling reached the slide, it came to rest in the angle formed by the glass plate and the edge of the slide. It remained there many minutes until disturbed.

Gravity. Exp. 17.—An adult female was placed in a glass tube which was enclosed in a black sleeve to exclude light, and the tube placed in a vertical position. The position of the thrips was marked with a wax pencil before putting on the sleeve. The sleeve was then removed momentarily at frequent intervals, and the position and direction of crawling of the insect noted. Most frequently it was found lower than the previous position,

and crawling downward. This was not always the case, however.

Of other specimens tried, some showed positive geotropism more definitely, some less definitely than the one described. None showed a negative reaction in the majority of cases.

Anaphothrips striatus

Light. Exps. 5 and 7.—Adults of this species were shaken out on a sheet of white paper near a window, and the course of their crawling was plotted as accurately as possible in my notes. Some individuals were decidedly negative to light, crawling directly away from the window every time they were tried, regardless of the direction in which they happened to be headed when they touched the paper. Others were indifferent to light, crawling in various directions. *Most of the males used were decidedly negative to light, females usually indifferent.*

Exp. 10.—Females taken from the exposed portions of leaves of *Spartina michauxiana,* and tested as above, were found in nearly every case to be *indifferent to light. Females from the curled young leaves of the same plants were as a rule negative to light.*

Exp. 6.—Larvæ were usually found indifferent to light, regardless of whether they came from exposed or concealed situations.

Exp. 15.—A single larva taken from the exposed part of a leaf, when placed in a glass tube one end of which was directed toward the window, crawled steadily toward the window. When the position of the tube was reversed, the larva at once reversed its direction. The tube was then placed in a black sleeve to exclude the light, and kept there for an hour. When it was removed, the larva showed for some minutes a *decidedly negative reaction to light.* Later, however, its behavior became indefinite, and *soon became markedly positive. Darkness had apparently temporarily reversed its reaction.*

Contact. Exp. 22.—A female of this species which was

negative to light was placed on a sheet of blotting paper. A small square of glass was placed over her, and supported at one edge, so that in crawling away from the window the thrips approached the edge of the glass which was in contact with the paper. She soon became lightly wedged between the glass and the blotter, and came to rest. Blotter, thrips and glass were then carefully turned through 180 degrees so that the negative reaction to light would have led the thrips out of its crevice; but she remained there for a long time. *Positive reaction to contact overcame the negative reaction to light.*

Another female, indifferent to light, was placed under a similar glass. In her random crawling she became wedged between the blotter and glass, and, notwithstanding that the blotter was occasionally turned in the meantime, *remained there several hours, until I lifted the glass.*

Another female, not negative to light, was placed under a similar glass square. She crawled from under it, but happened to crawl against the edge of the microscope slide that supported the glass cover. She settled quickly into the right angle formed by the slide and the blotter, and remained there a long time.

Gravity. Exp. 21.—A female which was indifferent to light was placed in a glass tube, and the tube set in a vertical position. The thrips immediately began to crawl downward. The tube was reversed, and the thrips immediately reversed its direction. A sleeve was placed over the tube to exclude the light, and frequently removed temporarily to observe the position of the thrips. In every case she was found crawling downward.

When the tube was held in an oblique position, the result was the same; the thrips crawled down the slope. If she was already crawling down, a slope of 5 to 10 degrees was found to be sufficient to keep her going in the same direction. But to reverse the direction of crawling, it was necessary to create a slope of about 45 degrees in the opposite direction. The same positive geotropism was shown when the thrips was placed on an inclined sheet of

paper; but being here at liberty to fly, she soon interrupted the experiment.

Numerous other females were tried, and all showed positive geotropism, some more promptly than others, but all perfectly definitely. A single male tested showed no definite reaction to gravity. A larva, nearly full grown, subjected to the same tests, showed as definite a positive reaction to gravity as did any of the females.

With the possible exception of the males, therefore, *Anaphothrips striatus is decidedly positive to gravity.*

Anthothrips verbasci

Light. *Exp. 4.*—Adults of this species, shaken out on a paper near a window, crawled in various directions. *None of them showed any definite reaction to light.*

Numerous larvæ, none of them over three fourths grown, *crawled directly away from the window in every instance.*

Exp. 12.—In this experiment adults from concealed places in mullein spikes were compared with those from exposed situations. They were shaken out on a sheet of paper near a window, and the direction of crawling noted. In every case, *those from concealed situations showed a fairly definite negative reaction to light.* Of those from exposed situations, *two were plainly negative, the remaining ten indifferent to light.*

Exp. 11.—Larvæ taken from concealment in a mullein spike were tested, on a sheet of paper, for their reaction to light. *Those of the smaller sizes crawled directly away from the window.* Those nearly full grown, while on the whole negative, crawled in a more or less devious path away from the window. One reddish larva, which from its color and size must have been *nearly ready to pupate, was especially indefinite in its reaction to light.*

Contact. *Exp. 18.*—Larvæ of various sizes, which were found to be negative to light, were placed on a blotter under a square of glass supported at one edge, as described for *Anaphothrips striatus.* When, in crawling

away from the window, they became wedged lightly between glass and blotter, and came to rest, the blotter with all on it was turned through 180 degrees. The larvæ turned their bodies so that their heads were directed away from the window, but did not crawl away. *The positive reaction to contact overcame the negative response to light.*

An adult tested in the same manner as the larvæ above described did not come to rest under the glass square. But happening to crawl against the microscope slide which supported the glass, the thrips came to rest in the right angle formed by the blotter and the edge of the slide, and remained there a long time.

Gravity. Exps. 13 and 20.—Adults and larvæ were put, one at a time, into a glass tube, which was set in a vertical position, and covered with a black sleeve to exclude light. Some were examined at frequent intervals, others were left half an hour without examination. In every case the thrips were found almost precisely where they were put at the beginning of the experiment. *This species is therefore indifferent to gravity.*

Anthothrips niger

Light. Exp. 2.—The red larvæ of this species were shaken out on a paper near a window, as described in other experiments. In every case the larva *crawled away from the window for a few seconds at first, then slowly turned toward the window, and continued indefinitely toward the light.* Once while the larva was crawling toward the light, I tapped the paper vigorously with a pencil, so that the thrips was lifted slightly from the paper and let drop; *it immediately reversed its direction, crawling from the window,* but in a few seconds turned again toward the light. The paper was jarred frequently, but always with the same result. To show whether the jarring made the response to light negative, or merely reversed whatever the larva was doing at the instant, the tapping was repeated at intervals of one or two seconds.

At the first tap, the larva, which had been crawling toward the window, immediately turned away from the light. Before it resumed its positive response to the light, the paper was tapped again; *the negative response continued.* In this way the larva could be kept crawling away from the light indefinitely. *Disturbance makes the reaction of the larva to light temporarily negative; otherwise it is positive.*

Summary of Experiments

Euthrips tritici, when disturbed, is positively phototropic in both larval and adult stages. It is positively stereotropic, and the stereotropism is stronger than phototropism, at least under certain circumstances. Some individuals appear to be on the whole positively geotropic; others are indifferent.

Anaphothrips striatus.—Adult males are usually negatively phototropic. Females taken from exposed situations are usually indifferent to light, those from concealed situations usually negative. The larvæ are usually indifferent to light, regardless of the kind of place from which they are taken; a single larva that was positive was made negative by keeping it in the dark. Adults are positively stereotropic. The females and larvæ are positively geotropic.

Anthothrips verbasci.—Adults taken from concealed situations are usually negatively phototropic, those from exposed places tend to be indifferent to light. The larvæ are all negatively phototropic, except the full-grown ones, which may be indifferent. The larvæ are plainly positively stereotropic, the adults less plainly so, or not at all. Neither adult nor larva responds to gravity.

Interpretation of the Experiments in their Relation to Distribution and Behavior of Thrips in Nature

With the evidence from these experiments before us, may we not interpret the observed distribution and behavior of the Thysanoptera in nature somewhat as follows? Instead of explaining the fact that *Euthrips tritici*

always lives in concealed situations as due to a demand for protection, we may assume that it is due to the strong positive stereotropism of this species—aided in some cases by positive geotropism, where the flower inhabited is upright, but notwithstanding positive geotropism where the flower is inverted. The rapid escape by crawling or flight when disturbed is not due to the fact that this is the best way of avoiding danger, but to the positive reaction to light. Other species avoid danger by going deeper into crevices, because they are negatively responsive to light.

Anaphothrips striatus lives on grasses doubtless because it can not live on any other food, or because the reproductive processes are not stimulated by any other host plant. But their distribution and behavior on the grasses may be explained largely in terms of their reactions to the three agents tested in the experiments. The males usually live in concealed situations on the plants (curled-up leaves) because they are mostly negatively phototropic, and crawl down the leaves until they reach these concealed situations. Females may live either in exposed or in concealed places, for some of them are negative to light, others indifferent. The larvæ are either exposed or concealed, because they are indifferent to light. The eggs from which they hatch are probably laid by negatively phototropic females in the young curled leaves, and the leaves unfold as the larvæ develop; this explains why the exposed larvæ are much larger, on the average, than are those concealed in the young leaves. Perhaps the relation of cause and effect as here stated is reversed, at least for some cases. Concealment—*caused* in one way or another—may lead to negative phototropism, as in the larva which was made temporarily negatively phototropic by being kept in the dark.

The adults are lodged between the ridges on the upper side of the leaves of the grass *Spartina,* not for the sake of protection, it seems to me, but because they are positively stereotropic. Doubtless between the ridges is the

place where they can best suck the juices of the plant, but there is no need to assume that they deliberately choose this location in order to get their food most easily. Both adults and larvæ rest on these leaves with their heads directed toward the base of the leaf, and crawl toward the base of the leaf if disturbed, not because protection is most quickly to be found among the curled leaves at the center of the plant, but because the thrips are positively geotropic.

Anthothrips verbasci.—The larvæ of this species live hidden among the flowers of the mullein spike, not because they must get their food there, for they can get it from any part of the plant; nor do they hide there, it seems to me, to secure protection. They remain in these crevices because, excepting the largest larvæ, they are positively stereotropic and negatively phototropic. The adults are sometimes exposed, sometimes concealed, probably because in the former case they are usually indifferent to light, in the latter case negatively phototropic. (Or may they be made negative or indifferent according as they live—for one reason or another—concealed or exposed?)

Thus, while *Anthothrips verbasci* is limited to one food plant, and the food requirements are therefore probably exceedingly important, yet the distribution and behavior of the insects on this plant may be explained without appealing to anything like "choice" in other matters.

Regarding *Anthothrips niger,* I wish to call attention to but one fact. The difficulty with which the larvæ are driven forth from a flower in which they live appears to be due, not to a persistent attempt at concealment, but to the fact that on being disturbed they are temporarily negatively phototropic; if the disturbance is continued, the negative response continues.

The only argument which, it appears to me, could be advanced in favor of assuming that the Thysanoptera choose their locations, instead of adopting simple response to external stimuli as the correct explanation of

distribution, is the possibility that they have learned that certain modes of behavior are best suited (for example) to continued safety.

The reply to such an argument is first, that most of my studies on behavior have been made in an unsettled region, where the enemies of thrips incident to civilization are practically wanting, and where even the natural enemies are not abundant. It could hardly be assumed that every individual would learn to avoid its enemies in the course of its short lifetime, yet certain species seem to be invariable in their response to certain agents. Furthermore, many of the larvæ tested in the experiments could have been but a few days old. It is incredible that their reactions should have been, as in fact they were, as definite and invariable as those of older larvæ, if these responses were dependent on experience.

It seems to me, therefore, that the only satisfactory explanation of outdoor behavior and distribution of the Thysanoptera lies in the assumption that they are in large measure the result of responses to simple stimuli, and do not imply any degree of choice.

Origin and Adaptiveness of Responses to External Stimuli

The origin of such responses in Thysanoptera as have been described above is not, I believe, discoverable. Purposeful they most probably are not, as I have shown, if by purpose we mean conscious direction of actions to some end. But adaptive they no doubt are in many cases. Perhaps they are all adaptive, but I confess that my powers of analysis are not keen enough to prove such a view correct. That *Euthrips tritici* is positively phototropic when disturbed is no doubt the cause of frequent escapes from danger. One may even believe the *negative* phototropism of larvæ of *Anthothrips verbasci* to be adaptive, because they are much more sluggish than is *Euthrips tritici,* and could not escape quickly even if they should emerge into the light. They are probably safest,

therefore, if, when disturbed, they retire into still deeper crevices. But I am unable to discover the adaptiveness of the response of the larvæ of *Anthothrips niger* to light —at first negative, on being disturbed, but soon becoming positive. Nor can I understand why the males of *Anaphothrips striatus* are more definitely negative to light than are the females or larvæ. These reactions seem to me to be useless.

We need not demand that all of these responses be adaptive, any more than that they be purposeful. Responses have arisen, no one knows how. They have been preserved, and we can but speculate as to the method of their preservation. Natural selection may be responsible for the preservation of the useful, and it may have eliminated responses that were harmful. But other responses of no value whatever, but likewise harmless, may have been allowed to persist, without help or hindrance from selection.

(*To be continued.*)

SHORTER ARTICLES AND CORRESPONDENCE

THE ENDEMIC MAMMALS OF THE BRITISH ISLANDS

When, in 1891, I was collecting information to be used by Dr. A. R. Wallace in preparing the second edition of his "Island Life," I found much skepticism among naturalists concerning the alleged endemic or precinctive elements of the British fauna. Dr. Wallace was able to give lists of supposed precinctive species and varieties belonging to several groups, but for the mammals he was obliged to state, "it is the opinion of the best authorities that we possess neither a distinct species nor distinguishable variety." We little imagined that about twenty years later the British Museum would issue a work describing ten species and twenty subspecies of mammals peculiar to the British Islands; twenty-one of these being actually undescribed at the time I made my enquiries, and the rest then reposing quietly in the synonymy. Still less did we imagine that such a revision, when made, would be the work of an American, coming over from the United States National Museum to show Europeans the neglected wonders of their own fauna! The Catalogue of the Mammals of Western Europe, by Mr. G. S. Miller, published last year by the British Museum, is certainly one of the most remarkable zoological works ever produced, and is well worthy of the attention of all naturalists, whether specially interested in the Mammalia or not. While so many students of genetics are giving us the results of their experiments in breeding mammals, it is worth while to turn also to the results of nature's long-time breeding experiments, so clearly set forth by Mr. Miller in the volume cited. What, after all, is the connection between the phenomena seen by the breeder and the facts of mammalian evolution? Do species and subspecies differ by "units," and do the variations observed in captivity correspond in any way to the recorded specific and subspecific differences?

A complete analysis of Mr. Miller's volume can not be made at the present time, but I have extracted the list, given below, of the forms supposed to be confined to the British Islands, giving their distribution and principal distinctive characters. I have added to Mr. Miller's list three quite recently described animals. On examining the list, it appears that a few of the species must belong to the older fauna of the country, not wholly exterminated by the glacial ice and periods of partial submergence. Such are

Mustela hibernica of Ireland and *Microtus orcadensis* of the Orkney Islands. It is at least suggestive, in this connection, that so many of the Scottish islands yield animals differing from those of the mainland. In the majority of cases, however, the peculiar British mammals are closely related to those of the continent, and might well be of very recent origin. There is a decided tendency to darker colors, such as has been noted also among British moths. In spite of this tendency, however, some forms are lighter than their relatives, the most conspicuous case being the light-tailed British squirrel. In several cases the difference noted has in part to do with particular phases; thus the squirrel has no dark phase, and the ermine does not turn so white in winter. The British red grouse, it will be remembered, is peculiar in lacking a white winter phase. Some of these differences may be due to the direct effect of the mild and moist British climate, and would perhaps disappear in the descendants of British animals taken elsewhere. The experiments on birds by Beebe are very suggestive in this connection. In other cases, the distinctions are such as might readily result from changes in one or two "units," such as are observed in experimental breeding. When we have a variable type, subject to losses and new combinations of unit characters, it is perhaps to be expected that different groups of individuals, isolated from one another, will after a time produce different homozygous combinations. That is to say, the result comes from a long series of "accidents," which will probably not be duplicated in two different places. In this way mere isolation may be an adequate cause of modification, providing always that through variation degrees of heterozygosity have arisen.

In the common house mouse, *Mus musculus,* Hagedoorn[1] has isolated and figured a great number of color varieties, for nearly all of which he has constructed zygotic formulæ. Little[2] has also described and figured a similar series of varieties, apparently in ignorance of Hagedoorn's paper, which he does not cite. He gives zygotic formulæ for thirty-two different varieties, but not all of them are visibly different. Albino varieties, resulting from the dropping out of a particular determiner, may be produced, corresponding in other respects to each of the thirty-two colored forms, although they all look alike, and will only show their true characters on crossing. Several of the varieties show

1 *Zeit. f. ind. Abst. Ver.,* 1912.

2 "Experimental Studies of the Inheritance of Color in Mice," 1913.

noteworthy fluctuating variability, due to differences in expression.

Mus musculus, then, is very conspicuously variable in color; yet Miller's book records only one subspecies, that of the Mediterranean region and the Azores, which is less dusky and more yellowish, with the under parts buffy grayish. It possibly agrees with Little's "dilute black agouti" variety. On the other hand, *M. musculus* has a recognized subspecies in Mexico, where it must have developed since the species was introduced by man. The mice of St. Kilda and the Faroe Islands, although given as distinct species, are derivatives of *Mus musculus,* differing in other points than color. In connection with subspecific differences in size, Sumner's experiments with different temperatures should be noted, since they prove that differences of temperature might lead to readily measurable differences in dimensions, wholly unconnected with losses of determiners or new zygotic combinations. Whether or not diverse conditions of this sort would ultimately affect the germ plasm, their effects would be patent long before and quite independently of any such modification. On the whole, the poverty of *Mus musculus* in subspecies would suggest that the variations observed by breeders are not, as a rule, the stuff that new subspecies are made of. Against this argument may well be adduced the fact that *M. musculus* is an urban animal, constantly traveling about, so that incipient races do not remain isolated. Here the closely related rats, *Epimys,* are worth considering. For Europe Miller can only recognize the Norway, Black and Alexandrian rats, all widespread, practically cosmopolitan. Yet in the Malay Archipelago, where *Epimys* is distributed over myriads of islands, large and small, the species are innumerable. One can almost take a map and indicate where new species of *Epimys* are to be found, namely, on those islands still unexplored. Years ago, when the writer was actively engaged in studying the British Mollusca and Lepidoptera, the question of endemic forms was constantly in mind; but in those days we failed to discriminate properly between the different classes of "varieties." We made the mistake of looking for well-marked "sports" or aberrations, rather than for constant but only slightly distinguished local races. There was a practical reason for this, in the fact that by searching the literature we could ascertain whether a well-marked variation had been reported from the continent; whereas the determination of subspecific types analogous to those described by Miller among

mammals required long series from different parts of Europe, and these we did not possess, and could not readily obtain. Miller, following the custom of mammalogists, lays great stress on subspecies, but almost ignores individual variations, except such as are expressed by the statistical data regarding size. By reading the synonymy, one can see that many such variations have received names, and I can not doubt that the time will come when these names will be generally used. In this case, it will be extremely desirable to use the same adjectival name for analogous varieties of different species, and beyond the limits of subspecies it ought not to be held that a name once used in a genus can not be employed again. It may be true that most or all of the "individual" varieties can be expressed by zygotic formulæ, but one can not remember all these formulæ, nor use them in speech with any comfort. Moreover, they have to do with the germinal constitution rather than the patent characters. Little provides all his varieties with polynomial English appellations, but would not Latin varietal names be better? Following his theory concerning the pigments, some of the varieties receive names which do not suggest the animals at all; thus "brown-eyed yellow," according to the apparently excellent colored plate, is light orange-ferruginous, while "sooty-yellow" is dark gray with yellowish under parts. Morgan[3] describes a wild variety of *M. musculus* from Colorado, which he calls "mauve," but from the detailed account it is rather "fauve," namely, fulvous or yellowish brown. It must be similar to the Old World subspecies *azoricus*, or possibly that subspecies introduced? If we had standard scientific names for the different forms, we should try to compare our specimens with the types or descriptions of those names, and it would not be left to authors to use such miscellaneous descriptive terms as might occur to them. For *Mus musculus*, possibly Little's apparently excellent colored plates might be made the standards for a series of names. Thus his Fig. 9 (pl. 3) is the animal named *niger* as long ago as 1801; Fig. 10, the dilute black, would naturally take the name *nigrescens*. Fig. 12 is probably *albicans* of Billberg, 1827.

MAMMALS PECULIAR TO THE BRITISH ISLANDS

Insectivora

Sorex araneus castaneus (Jenyns 1838). Great Britain. Not so dark as true *araneus*.

[3] *Ann. N. Y. Acad. Sci.*, XXI, p. 106.

Sorex granti (Barrett-Hamilton and Hinton 1913). Inner Hebrides. Differs from *araneus* by the contrast between bright-colored flanks and dusky upper parts; teeth also different.

Neomys fodiens bicolor (Shaw 1791). Great Britain. Under parts usually washed with wood-brown instead of buffy whitish; skull smaller.

Chiroptera

Rhinolophus ferrum-equinum insulanus Barrett-Hamilton 1910. Central and S. England. Wing shorter.

Rhinolophus hipposideros minutus (Montagu 1808). England and Ireland. Wing shorter.

Carnivora

Mustela erminea stabilis (Barrett-Hamilton 1904). Mainland of Great Britain. Rather large, with large teeth; color somewhat different, a little darker above. Change to white in winter less complete and regular than in continental forms.

Mustela erminea ricinæ (Miller 1907). Islands of Islay and Jura, Scotland. Smaller than *stabilis;* proportions of skull different.

Mustela hibernica (Thomas and Barrett-Hamilton 1895). Ireland and Isle of Man. Quite distinct; recognized by combination of black-tipped, heavily penciled tail with entirely dark ear and upper lip. Superficially like certain North American forms.

Felis sylvestris grampia (Miller 1907). Scotland; formerly throughout Great Britain. Darker, with more pronounced black markings.

Rodentia

Lepus europæus occidentalis de Winton 1898. England, Scotland and Isle of Man. Buffy tints rich and dark.

Lepus timidus scoticus (Hilzheimer 1906). Highlands of Scotland. Smaller; rarely becomes so white in winter as Alpine race.

Lepus hibernicus Bell 1837. Ireland. Distinguished by the strongly russet color and partial or complete absence of white winter coat. Larger than *scoticus.*

Evotomys alstoni Barrett-Hamilton and Hinton 1913. Island of Mull, Hebrides.

Evotomys glareolus britannicus (Miller 1900). Great Britain. Smaller; color less intense.

Evotomys skomerensis Barrett-Hamilton 1903. Skomer Island, off coast of Wales. Color above unusually light and bright; skull peculiar.

Microtus agrestis exsul Miller 1908. North and South Uist, Hebrides. Resembles true *agrestis* of Scandinavia; teeth peculiar, a character usually present which elsewhere in the species occurs as a rather rare anomaly.

Microtus agrestis macgillivraii Barrett-Hamilton and Hinton 1913. Island of Islay, Hebrides.

Microtus agrestis hirtus (Bellamy 1839). England and South Scotland. Smaller than typical *agrestis;* upper parts noticeably tinged with russet, and venter washed with wood-brown.

Microtus agrestis neglectus (Jenyns 1841). Highlands of Scotland. Not so small as *hirtus;* upper parts darker.

Microtus orcadensis Millais 1904. South Orkney Islands. Related to *M. sarnius* of Guernsey and the Pleistocene *M. corneri* of South England. Distinguished by its large size and dark color.

Microtus sandayensis (Millais 1905). Sanday Island, N. Orkney group. Allied to *orcadensis,* but skull differing; upper parts much lighter.

Microtus sandayensis westræ Miller 1908. Westray Island, N. Orkney group. Not so pale as in typical form; teeth differing a little.

Arvicola amphibius (L. 1758). Typical subspecies. England and South Scotland. Large; color moderately dark.

Arvicola amphibius ater (Macgillivray 1832) = *reta* Miller 1910. Scotland, except southward. Darker, melanism frequent. The name was changed on account of *Hypudæus terrestris* var. *ater* Billberg 1827, but the change is perhaps needless, as Billberg's animal was not a subspecies, and has not been treated as a species or subspecies under *Arvicola.*

Apodemus hebridensis (de Winton 1895). Lewis and Barra islands, Hebrides. Large, with small ears; color dark.

Apodemus hirtensis (Barrett-Hamilton 1899). Island of St. Kilda. Near *hebridensis,* but skull larger and color darker.

Apodemus fridariensis (Kinnear 1906). Fair Isle, Shetland group. Large; skull peculiar; colors also somewhat peculiar.

Apodemus flavicollis wintoni (Barrett-Hamilton 1900). England. Under parts with duller color, pectoral spot more diffuse.

Mus muralis Barrett-Hamilton 1899. Island of St. Kilda. Like *M. musculus* but feet and tail less slender; skull peculiar.

Mus færoensis (Clarke 1904). Faroe Islands. Larger than *musculus* and *muralis;* hind foot very robust; tail thickened.

Sciurus vulgaris leucourus Kerr 1792. Great Britain and Ireland. Small; tail drab, fading in summer to cream buff. No dark phase.

Ungulata

Cervus elaphus scoticus Lönnberg 1906. Great Britain. Color darker and less gray than in the related Norwegian form.

Capreolus capreolus thotti Lönnberg 1910. Great Britain. Darker, face darker than body.

I thought it of interest to compare the above British list with a similar one for the Spanish peninsula (Spain and Portugal). The latter area is continuous northward with France, but the Pyrenees constitute a barrier. The Iberian peninsula differs so much in its recent geological history from Britain, and is at the same time so much more southern, that we should expect to find the faunal elements very different. This expectation is realized, yet the difference in numbers between the two lists is not very great, and the number of Iberian forms treated as distinct *species* is exactly the same (12) as that for the British Islands. This suprising result is evidently due to the numerous small

islands of the British group, such islands being wanting around the coasts of Spain.

MAMMALS PECULIAR TO THE SPANISH (IBERIAN) PENINSULA

Insectivora

Talpa occidentalis (Cabr.).
Galemys pyrenaicus rufulus (Graells.).
Sorex araneus granarius Miller.
Neomys anomalus Cabr.
Crocidura mimula cantabra (Cabr.).
Crocidura russula cintræ Miller.
Erinaceus europæus hispanicus B.-Ham.

Chiroptera

(None.)

Carnivora

Canis lupus signatus Cabr.
Canis lupus deitanus Cabr.
Meles meles marianensis (Graells.).
Martes foina mediterranea (B.-Ham.).
Mustela nivalis iberica (B.-Ham.). (Also Balearic Is.).
Mustela putorius aureolus (B.-Ham.).
Mungos widdringtonii (Gray).
Genetta genetta (L.), typical subsp.
Felis sylvestris tartessia (Miller).
Lynx pardellus Miller.

Rodentia

Lepus granatensis Rosenb. (Also Balearic Is.).
Lepus granatensis gallæcius Miller.
Eliomys lusitanicus (Reuvens).
Glis glis pyrenaicus Cabr.
Microtus agrestis rozianus (Bocage).
Microtus asturianus Miller.
Arvicola sapidus Miller, typical subsp.
Pitymys lusitanicus (Gerbe).
Pitymys mariæ (Major).
Pitymys pelandonius Miller.
Pitymys depressus Miller.
Pitymys ibericus (Gerbe), typical subsp.
Pitymys ibericus centralis Miller.
Pitymys ibericus pascuus Miller.
Pitymys ibericus regulus Miller.
Mus spicilegus hispanicus Miller.
Mus spicilegus hispanicus Miller.
Sciurus vulgaris numantius Miller.
Sciurus vulgaris infuscatus (Cabr.).
Sciurus vulgaris seguræ Miller.
Sciurus vulgaris bæticus (Cabr.).

Ungulata

Sus scrofa castilianus Thomas.
Sus scrofa bæticus Thomas.
Cervus elaphus hispanicus Hilzh.
Capreolus capreolus canus Miller.
Capra pyrenaica lusitanica (França).
Capra pyrenaica victoriæ Cabr.
Capra pyrenaica hispanica (Schimp.).
Rupicapra parva (Cabr.).

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NOTES AND LITERATURE

SWINGLE[1] ON VARIATION IN F_1 CITRUS HYBRIDS AND THE THEORY OF ZYGOTAXIS

Swingle in two recent papers has published some very interesting observations on *Citrus* species and their F_1 hybrids. On the basis of these observations, the somewhat startling statement is made that current theories of heredity and variation give no adequate explanation of variability in F_1 hybrid generations from "pure bred" parent strains. Swingle assumes this variability to be so great that qualitative differences in chromosomes can not account for it. As the chromosomes in the F_1 hybrid remain unfused until synapsis, there is said to be no opportunity for quantitative exchange of hereditary substance, so that this variation can not be accounted for on this basis. Hence,

> if proof can be given to show that in certain specific cases, pairs of gametes of *identical hereditary composition*[2] give rise to very diverse organisms, the way has been opened for a general reinvestigation of the validity of our modern theories of heredity.

The term "pure bred" as used by Swingle implies that certain *Citrus* species reproduce themselves in a relatively faithful manner from seed, there being no overlapping of distinguishing specific characters and very little variation of these characters intraspecifically. *C. aurantium* and *C. trifoliata* are examples of such widely separated species. The former has been grown from seed in Florida for two hundred years, and though variations have appeared, they are said to differ but little from the general type of *C. aurantium,* and in no way to approximate that of *C. trifoliata.*

On the basis of evidence of this kind, Swingle believes the various *Citrus* species (*C. aurantium, C. trifoliata, C. medica limonum,* etc.) breed true in nearly all their characters and especially in those which differentiate them from one another. Hence, for genetic studies, the germ cells of these species are

[1] Swingle, W. T., "Variation in First Generation Hybrids (Imperfect Dominance): Its Possible Explanation through Zygotaxis," IV° Conf. Internat. de Genetique, Paris, 1911, pp. 381–394; "Some New Citrus Fruits," *Amer. Breed. Mag.,* 4: 83–95, 1913.

[2] The italics are my own.

assumed, in respect to these differential characters, to be pure; or, expressed in more technical language, each species is for the characters under observation, genotypically homozygous. This assumption is based on wholly inadequate evidence, as will be shown later.

Citrus trifoliata crossed with other *Citrus* species (*C. aurantium*, etc.) gave F_1 hybrid families showing a large degree of variability, even when the seeds from a single cross having identical male and female parents were grown. This variability expressed itself in foliage, habit of growth, and fruit, and was especially noticeable in the latter, the fruits of the F_1 individuals showing differences in color, size, texture, shape, number of seeds, and flavor. For example, from a single cross of *C. trifoliata* × *C. aurantium*, the 11 resulting hybrid seeds gave rise to F_1 plants (citranges) differing in foliage, habit of growth, and very strikingly in fruit. The fruit of one of these citranges, the "Morton," was smooth, round, very large, and orange-colored; those of the "Colman" were rather flattened, globose, pubescent, yellow, almost seedless, and lacked the disagreeable oil common to the others; while those of still another type, the "Willits," were often monstrously fingered. The "Phelps" was bitter, while the "Saunders" almost lacked this quality. The "Rustic" often has double fruits with many seeds, and a habit of growth more like its *aurantium* parent.

When varieties of the lemon were crossed with *C. trifoliata*, still greater differences in the F_1 generation (citremons) resulted. These consisted largely of "abnormal" foliage developments. Hypophylls, though absent in the common *Citrus* species are extremely characteristic of *C. trifoliata*. About 20 per cent. of the lemon-trifoliata hybrids developed an intensified form of this character, and this proportion occurred in each case in crosses involving three different varieties of lemon. The tangerine orange × grape fruit (tangelo) in the F_1 generation was almost as variable as the citrange families. F_1 hybrids between the West Indian lime and the kumquat (limequat) were strikingly different in such characters as aroma, flavor, acidity of pulp and thickness of skin.

Although much stress has been laid on the differences in these F_1 hybrids, there were numerous similarities. For example, all the *Citrus* hybrids involving *C. trifoliata* in their parentage have compound, semi-evergreen leaves, increased hardiness and fruits

with abundant bitterish, acid juice. Two of the citranges (Colman and Cunningham) have the pubescent fruit character of *C. trifoliata,* while the others are smooth-skinned.

The author's data led him to formulate in substance the following conclusions, which I have grouped and stated in my own language.

1. *Citrus* species are but slightly variable in the characters which differentiate them, and, in the sense that no overlapping takes place, may be said to breed true, their germ cells being genetically pure for these differential characters.

2. Individual plants of the F_1 hybrid generations between these species are strikingly variable, although all are, in a given cross, the zygotic product of *pairs of gametes* of *"identical hereditary composition."*

3. Modern theories of heredity can not account for this variation.

These are not the conclusions, however, in which all present-day geneticists would concur. In the first place, few "modern" geneticists would take Swingle's view concerning the "pure breeding" ability of the various *Citrus* species, nor even of *C. aurantium.* Webber, in the Encyclopedia of American Horticulture, notes that 70 varieties of the common sweet orange are grown within our borders, and although a few varieties are fairly constant, the majority of these do not breed true from seed. Practically the same idea has been gained by certain prominent taxonomists of the genus *Citrus.* De Candolle specifically calls attention to the remarkable variability of the whole group; and Professor Hume of Florida remarks on the same fact in certain Experiment Station publications. As to the variability among the individuals in the special strains used by Swingle in his breeding work, no data are given, so that it can not be affirmed that inbred progeny from them would have been duplicates as far as hereditary characters are concerned. *Citrus* plants naturally cross fertilize, and from this cause alone no dependence can be placed on their ability to produce progeny, which are exact duplicates of themselves when inbred; in fact, the inference is that they would not. Hence, as far as intraspecific constancy of hereditary characters is concerned, Swingle's statement can not be accepted until more exact information is produced.

Swingle says no interspecific gradations occur between these various species, especially *C. trifoliata* and *C. aurantium.* Grant-

ing this, the two species have clearcut differences in leaves (evergreen or deciduous, unifoliolate or compound), in resistance to cold (difference in ability to withstand certain degrees of temperature) and in numerous fruit characters (presence or absence of pubescence, quality of juice, quantity of seed, size of fruit, etc.).

From the standpoint of modern theories of heredity as regards variation in F_1 hybrid generations, it matters little whether so-called species intergrade or whether their differences are clear-cut and all variation is intraspecific. In either case, if crosses were made, variation among the F_1 individuals from a single family might or might not occur. In either case, no violence to modern theories of heredity would result and no new problems would arise. But if two species that differ from each other in part or all of their characters, but breed true intra-specifically (genotypically homozygous) are crossed, and F_1 variation results, then modern theories of heredity would be compelled to change front and invoke the aid of new hypotheses. Swingle's data, assuming that intraspecific variation in *Citrus* species occurs, does not present a problem of this kind at all. *C. aurantium* and *C. trifoliata* each possess distinctive characters, but convincing data are not at hand to warrant any belief in the homozygosity of these differential characters or of even those the two species may have in common. The evidence directly, and one might almost say conclusively, opposes such a conclusion. If these species are not homozygous in all of their characters, then one can not affirm, in the light of modern theories, that all the gametes produced by a particular group of individuals called a species are identical in hereditary composition, nor even that the gametes of one individual of such a species are identical as to hereditary potentialities. At the risk of wasting valuable space by repeating what is extremely common knowledge to genetic students, let us assume, for the purpose of argument, that *C. aurantium* and *C. trifoliata* are homozygous in all their respective characters except one. In the former, the character *A* is heterozygous and peculiar to this species. Likewise, in *C. trifoliata, B* is heterozygous and differential. All the remaining characters of the two species may be symbolized, respectively, by the formulæ *XX* and *YY*. When *XXAabb* (*C. aurantium*) is crossed with *YYaaBd* (*C. trifoliata*), the resulting progeny would appear in the approximate proportion of 1 *XYAaBb* : 1 *XYAabb* : 1 *XYaaBb* : 1 *XYaabb*, providing

A and *B* are single factor characters. In the majority of characters, the F_1 hybrids would be intermediate or possess those of either one or the other parent, since all the F_1 individuals would be alike as far as any hereditary quality symbolized by *XY* is concerned, providing the plants were all grown under the same environmental conditions. But these F_1 individuals would not be alike as regards the inheritance of the characters *A* and *B*. Experimental evidence from crosses of this kind show us that four different F_1 forms may result, the distinctions between them arising from the presence or absence, through inheritance, of the characters *A* and *B*. Dominance is assumed to be absent in this illustration.

Swingle's *Citrus* hybrids, though involving greater complexity because a large number of parental characters instead of two are probably heterozygous, are of the same general type as those of the illustration and lend themselves to the same interpretation. Owing to the absence of sufficient exact experimental data, one can not speak of unit characters and factors in these hybrids, but one may say without violence to modern theories of heredity that one or both of the parents involved in the crosses which produced the Colman and the Cunningham were heterozygous in the factors or factor for pubescence, that various size factors were heterozygous and that one parent was homozygous for absence and one for presence of the factors for hardiness, compound leaves and evergreen foliage.

F_1 variation in *Citrus* hybrids then, in the light of the data at hand, apparently results from differences in the gametic composition of the heterozygous parents.

Swingle calls attention to other cases of variation in F_1 hybrids from two pure stocks which support his contention that this phenomenon of F_1 variation is very general, though usually obscured through variation due to heterozygous parent stock. Collins and Kempton[3] crossed a race of corn breeding true to waxy endosperm with one constant for horny endosperm. Horny endosperm was dominant in F_1 and the F_2 generation segregated in the expected ratio of 1 waxy to 3 horny kernels. This ratio represented the average proportion of each when the ears of all the plants were lumped together. The F_2 progeny of each selfed

[3] Collins, G. N., and Kempton, J., II, 1912, "Inheritance of Waxy Endosperm in Hybrids of Chinese Corn," IV° Conf. Internat. de Genetique, 1911, p. 347; also Circ. No. 120, Bur. of P. I., U. S. Dept. of Agr., 1913.

F_1 plant when taken by itself gave some ears as low as 13.7 per cent. waxy, while others exceeded the expected proportions and gave ears as high as 33.3 per cent. waxy. The investigators point out that this variation is not the result of the laws of chance as the deviation is far greater in many cases than the probable error. Therefore, says Swingle,

> there can be no doubt but that their varying percentages represented real differences in the hereditary composition of the first generation plants. It would be hard to find a more conclusive case since there could be no doubt as to the purity of the parents and what is more rare no possible doubt as to whether a given kernel had a waxy or a horny endosperm.

Mendelians are said to be unaware how fatal this phenomena is to some of the chief tenets of modern theories of heredity, and they are also accused, somewhat unjustly, I believe, of applying the term "imperfect dominance" to this and to the *Citrus* phenomena.

In this case, both parents were undoubtedly homozygous for their respective endosperm characters, so that heterozygosity will not account satisfactorily for the deviations. But this is a different phenomena than Swingle found in his *Citrus* hybrids, for here one is dealing with a fluctuation in a proportion or ratio involving the same character, while in his experiments the difficulty was the variation in presence and absence of distinct and often new characters, indicating an extremely heterozygous parentage.

As an explanation or working hypothesis for his own and similar data, Swingle advances a somewhat new and suggestive chromosome theory on the assumption that it fills an urgent need. The theory of zygotaxis, as it is called, may be summarized as follows:

Maternal and paternal chromosomes probably persist side by side in the cells, unchanged in quality and number throughout the whole development of the F_1 organism. This being true, Swingle, in order to explain his data, assumes that the influence in character formation exerted by chromosomes on the F_1 hybrids, is in some cases due to their relative positions in the nucleus, and that these relative positions result from accident or at least are determined at the moment of nuclear fusion in fertilization, and remain unchanged in succeeding cell generations. He further

assumes that those chromosomes lying nearest the nuclear wall (peripheral) are better nourished than those centrally located, and hence they exert more influence in character formation, and dominating synapsis, produce gametes similar in their hereditary character to the cells of the first generation hybrids, whose character in turn was determined at fertilization by the configuration the chromosomes took in the fusion nucleus. On this theory, reversions, sports, etc., may result from sudden changes in the nuclear configuration.

Three types of nuclear configuration are assumed to occur in higher organisms, the character and effects of which are synoptically outlined below.

1. *Interspecific Hybrids.*—Usually sterile and intermediate. Chromosomes repel each other and occupy opposite sides of the F_1 zygote nuclei, exerting equal influence in the ontogeny of F_1 organisms, explaining why first generation hybrids of this character are always intermediate, little variable and usually sterile. Synapsis often impossible.

2. *Mendelian Crosses.*—Abnormally inbred races of domesticated animals and plants. F_1 generation usually intermediate, fertile, dialytic at synapsis. Dominance of certain characters in these hybrids is due to the inherited potentialities of the chromosomes rather than to their nuclear positions.

3. *Normal Cross-bred Species.*—Probably normal in wild species. Hybrids usually vigorous, fertile, and variable. Free intermingling of chromosomes in the fusion nucleus at fertilization. Nuclear configuration permanent for each individual. Synapsis normal.

This elaborate and attractive theory, based admittedly to a great degree on assumptions, is advanced by Swingle in the belief that it will help to clarify the problems of heredity, even though he acknowledges it does not help one to arrive at satisfactory explanations. In the reviewer's opinion, however, the field of genetics is already burdened with enough theories of this particular type and the somewhat unnecessary but ever-increasing new additions serve to confuse rather than clarify the ideas of the average student of genetics. Besides, Swingle's assumption that maternal and paternal chromosomes in the cells of F_1 hybrids repel each other and do not mingle in the F_1 zygote cells is not borne out by the few cytological facts at our command. Rosen-

berg's[3] work on species hybrids of *Drosera*, Moenkhaus's[4] investigations of species hybrids in fish and some work on certain hybrids in the Echinodermata group give us facts that directly oppose such an assumption. As a further criticism, one may say that most biologists who have had experience with pedigree cultures would decidedly criticize the synoptic outline and the narrow sphere assigned to Mendelian phenomena.

Aside from the theoretical considerations, these two papers contain descriptions of *Citrus*-like species new to occidental horticulture, together with a somewhat detailed account of the various *Citrus* hybrids and their hardiness and practical value, showing the truly fine results achieved by the workers in this field toward moving the *Citrus* belt northward and adding *new* varieties of this genus to the world's horticulture.

Orland E. White

Brooklyn Botanic Garden,
December 4, 1913

[3] Rosenberg, O., "Cytologische und Morphologische Studien an *Drosera longifolia* × *D. rotundifolia*," Kungl. Svenska Vetenskapsakademiens Handlinger., 43, N: ou, pp. 1–64, 1909. 4 Tafn.

[4] Moenkhaus, W. J., "The Development of the Hybrids between *Fundulus heteroclitus* and *Menidia notata* with especial reference to the Behavior of the Maternal and Paternal Chromatin," *Amer. Jour. of Anatomy*, 3: 29–65, 1904. Plates I–IV.

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THE ORIGIN OF × CAPSELLA BURSA-PASTORIS ARACHNOIDEA

DR. HENRI HUS

University of Michigan

Since Jordan[1] described a number of elementary species of *Capsella Bursa-pastoris*, their constancy has been a subject of cultural experiment. Herbarium material demonstrates the existence of numerous apparently undescribed forms. The finding of strikingly distinct forms, such as *Capsella Heegeri*[2] and, more recently, *C. Viguieri*,[3] the work of Almquist[4] and that of Shull have added to the interest which this species holds for the investigator. It was Shull who determined the zygotic constitution of various forms. To be able to demonstrate this with exactitude is of the greatest value since Bateson and Lotsy expressed their doubt as to the homozygocity of de Vries's *Œnothera Lamarckiana*. It was left to Nilsson[5] to clearly show its necessarily heterozygous character. The interest aroused by this paper[6] leads me to believe that an

[1] Jordan, A., "Diagnoses d'espèces nouvelles ou méconnues pour servir de matériaux à une flore réformée de la France et des contrées voisines." Paris, 1864.

[2] Solms-Laubach, H. Graf zu, "Cruciferen studien. I. *Capsella heegeri*, eine neuentstandene Form der deutschen Flora," *Bot. Zeit.*, **55**: 167, pl. 7, 1900.

[3] Blaringhem, L., "Les transformations brusques des êtres vivants." Paris, 1911.

[4] Almquist, E., "Studien über die *Capsella Bursa-pastoris* (L.)," *Acta Horti Bergiani*, **4**: No. 6, 1907.

[5] Heribert-Nilsson, N., "Die Variabilität der *Œnothera Lamarckiana* und das Problem der Mutation," *Zeitschr. f. ind. Abst. u. Vererb.*, **8**: 89, 1912.

[6] Lotsy, J. P., "Fortschritte unserer Anschauungen über Deszendenz seit Darwin und der jetzige Standpunkt der Frage," *Progressus Rei Botanicæ*, **4**: 361, 1913.

account of certain cultures of *Capsella,* in which mutations were simulated, would be of timely interest.

During the winter of 1908–1909, I collected in a greenhouse at Ann Arbor, Michigan, and at the disposal of the Botanical Department of the University of Michigan, twelve rosets of *Capsella Bursa-pastoris,* the leaves of which showed certain more or less striking morphological differences. With the hope of isolating certain biotypes, the rosets were placed in pots and permitted to flower. No measures were taken to prevent the accidental transference of pollen, but the pots were placed about six inches apart. This, as will be shown later, is the only precaution necessary to guard against cross-pollination, provided the cultures are carried on in a greenhouse and during the winter months. After a portion of the seed had ripened, the plants, the majority of which retained their climax leaves, became herbarium specimens. More recently, after constant association has enabled me to detect minute differences, it has been possible to identify some of these plants with two of the biotypes described by Shull,[7] to wit, *rhomboidea* and *simplex.* At the time of collection, the differences were sensed, but could not be described technically, since the extent of the influence wielded by fluctuating variability was an unknown quantity. Never before had I so fully realized the truth of de Vries's statement.[8]

> We are trained to the appreciation of the differentiating marks of systematic species. . . . Our minds are turned from the delicately shaded features which differentiate elementary species.

The seed obtained was sown in sterilized soil during the spring of 1910. From each seedpan 60 individuals were transplanted to flats. As the plants grew older, it was found that, with a single exception, the seedlings in each of the flats were uniform, but that the seedlings in the different flats were not alike, three types being distinguishable. The interest in these types, for the isola-

[7] Shull, G. H., "*Bursa bursa-pastoris* and *Bursa Heegeri:* Biotypes and Hybrids," Publ. No. 112, Carnegie Institution of Washington, 1909.

[8] de Vries, Hugo, "Species and Varieties," 689, 1905.

tion of which these cultures had been undertaken, soon was overshadowed by the behavior of the seedlings bearing the number 4,108.6 and which were the offspring yielded by a plant of a type not described by Shull and which I have named × *Capsella Bursa-pastoris Setchelliana,* in honor of Professor William Albert Setchell.

FIG. 1. APPEARANCE OF A LINEAR-LEAVED FORM AMONG SEEDLINGS OF *Capsella Bursa-pastoris.*

During the time that the seedlings remained in the seed-pan, no deviations from the expected course of development were noted. However, after the seedlings had been transplanted to flats and had remained there a week or so, it became evident that some of the seedlings were not making the expected growth. Their development appeared most insignificant compared with that of the majority. A closer examination showed the cotyledons to be somewhat larger than normal and the leaves proper to be exceedingly small and almost linear. Nor did they attain the same length as the leaves of the rosets belonging to other types.

An explanation of this peculiar development was sought in a possible attack on the part of either fungi or bacteria or in soil conditions. But the latter were uniform for the entire flat. Neither fungi nor bacteria could be demonstrated nor did the underground portion of the "abnormal" plants look unhealthy or underdeveloped.

FIG. 2. SEEDLINGS OF *x C. . . . Setchelli* AND *x C. . . . arachnoidea*

At this stage the flat presented the appearance shown in Fig. 1. At the time but three types were distinguished, the first of these constituted by plants which showed an incision of the blade, the second composed of those which apparently had entire leaves, and a third, comprising the small and linear-leaved rosets, which, because of the spider-like appearance of the latter, has been designated ×*Capsella Bursa-pastoris arachnoidea.* There also appeared a

single individual which, while closely resembling the form *arachnoidea,* differed from it in having somewhat spatulate leaves. This plant, a plant of *arachnoidea* and two of *Setchelliana,* are shown in Fig. 2.

After photographs had been taken, the plants were potted and placed in the frames. None of the plants made a growth as vigorous as that of the Capsellas growing in the open. The plants of the form *arachnoidea* developed leaves with a greatest length of 15 mm. and a greatest width of a little over 1 mm., causing the plant to retain its spider-like appearance. The roset with spatulate leaves appeared somewhat more vigorous, the average leaf measuring 22 mm. in length, with a greatest width of 2.5 mm. In later generations I have been able to obtain rosets of *arachnoidea* with a greatest leaf-length of 100 mm. and a greatest width of 6 mm.

In the frames, flowering shoots made their appearance, those on *arachnoidea* being remarkable chiefly because of their small size, reaching a length not exceeding 12 cm. The flowers were small but well-formed. No well-developed pollen could be demonstrated. Seed did not form and the capsules retained their original form, typical of non-fertile capsules in *Capsella Bursa-pastoris,* reminding one of the capsules of *Capsella Heegeri.* They do not resemble the fertile capsules of *C. procumbens.* In the next generation I saw a single capsule formed on *arachnoidea* as the result of cross-fertilization, and in this case it differed in no manner from the normal capsule such as we know it in *Capsella Bursa-pastoris.*

The "normal" plants, *i. e.,* all those not belonging to the form *arachnoidea,* matured a large amount of seed. No measures were taken to prevent cross-pollination, but no other plant of *Capsella Bursa-pastoris,* within a radius of twenty feet, was in flower.

At this time, another attempt was made to group the plants. It was found that the criterion used earlier, *i. e.,* the incision of the blade, no longer could be relied upon, since plants, which at the time of the previous count, had shown an entire margin, now were more or less incised.

Unfortunately, after the seed had been collected, the plants were destroyed, having lost their climax leaves. An attempt to group them later with the aid of photographs failed, because photographs of all plants were taken during the earlier stages only, *i. e.*, before the appearance of the climax leaves. Another classification, for which climax leaves are not essential, and which is based upon the relative width of the first six or eight leaves, yields for 54 plants the proportion: "wide" 31, "narrow" 16, "linear" 7, the ideal proportion, as since worked out, being 33 : 16 : 16. The fact that the number for "linear," which represents the form *arachnoidea*, is too small by 9, may be ascribed to various circumstances, among others the fact that the last row in the flat did not appear in the photograph upon which the count was based. It is in the last row of a flat one ordinarily meets with the smaller or at least less vigorous individuals and it is very probable that in this last row occurred a large percentage of individuals belonging to *arachnoidea*. Furthermore, not all the seedlings, but only sixty, were taken in each case. Almost unconsciously one selects the largest individuals when transplanting from seedpan to flat. It is probable that in this process there were eliminated a greater percentage of seedlings of the linear form than of any of the others. Hence no great weight can be attached to the proportion obtained.

The collection of seed brought the work for 1910 to a close. As far as I was aware, no forms similar to *arachnoidea* had been either noted or described by any one who had devoted his time to culture experiments with *Capsella*. Neither Shull in America, nor Almquist in Sweden, nor Lotsy[9] in Holland, has made mention of such forms in their publications. The fact that no seed was produced by the aberrant form seemed to hold out little hope for the continuation of the cultures, and the sole trace left by this new form, if taxonomic form it was, threatened to consist of but a few photographs and some alcohol specimens. A single possibility presented itself.

[9] Lotsy, J. P., "Vorlesungen über Deszendenztheorien." 1: 180, Jena, 1906.

Whether the parent plant was of a hybrid character or whether the parent plant was mutating, and the new form or forms were to be looked upon as mutants, in either case there existed the possibility, if not the probability, that from the seeds obtained from those plants of the second generation which appeared "normal," a third generation might be obtained which would again present the abnormal form. Such indeed proved to be the case.

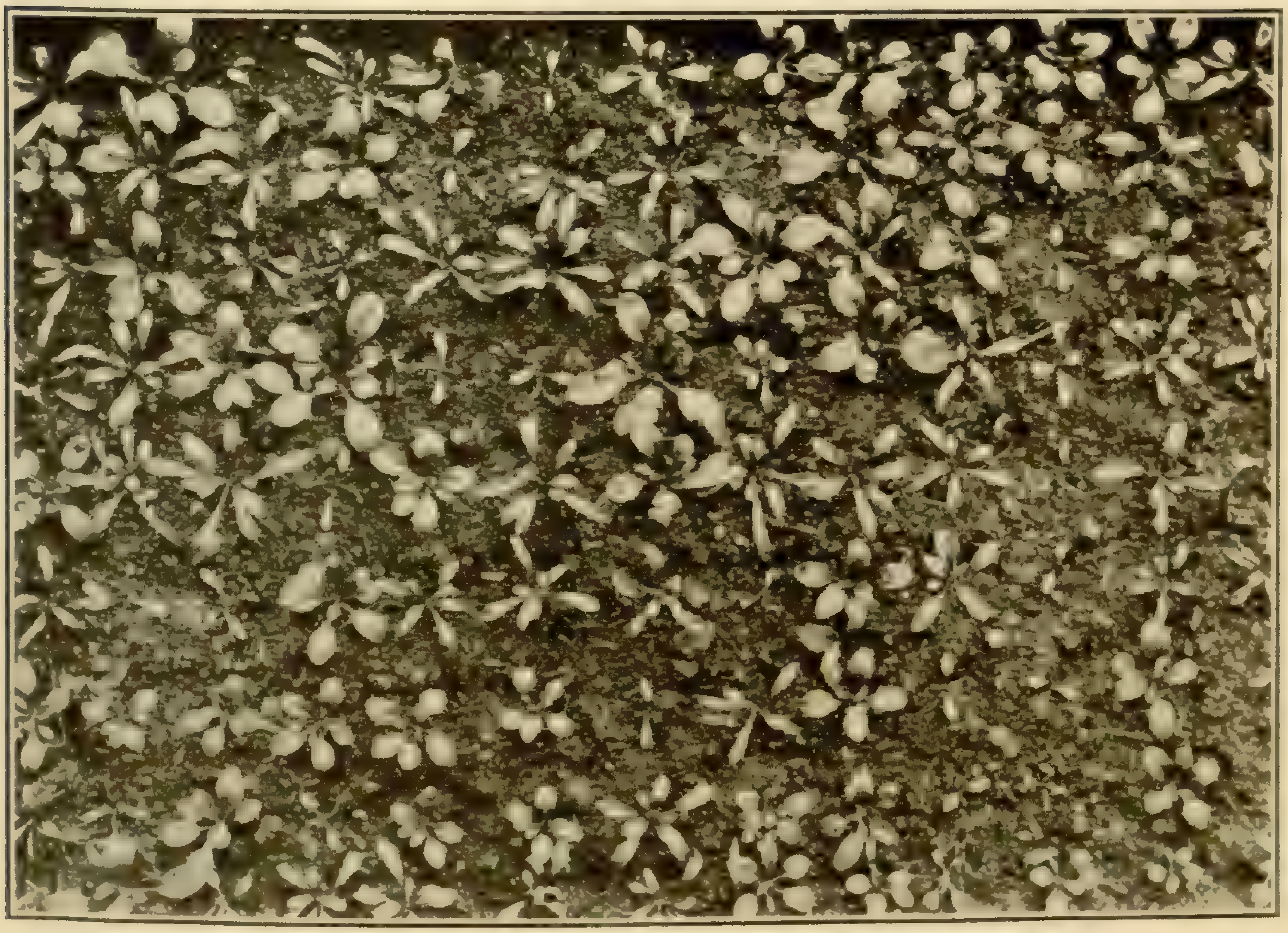

FIG. 3. EARLY STAGES IN THE DEVELOPMENT OF BROAD-LEAVED, NARROW-LEAVED AND LINEAR-LEAVED FORMS OF *Capsella*.

The seed for the next generation was obtained from 19 plants. The seed was sown separately in pots of sterilized soil. Certain of the parent plants, which we now identify with Shull's *simplex* and *rhomboidea*, produced a uniform, broad-leaved offspring. Others behaved like the parent, the form *arachnoidea* appearing in 197 individuals out of a total of 979, which does not include the 713 which bred true to the broad type. (For an illustration of these types see Fig. 3.)

It is unnecessary to go into details as to the various theories which suggested themselves as a solution of the

origin of the linear-leaved form which, because of its striking appearance, concentrated the attention upon itself. That perhaps we were dealing with a mutation was a thought which most naturally obtruded itself upon the mind of one who, for years, had fruitlessly tested a large number of species in the hope of discovering a case analogous to that of *Œnothera Lamarckiana*.[10] The possibility of a cross between a local form and either *Capsella Heegeri* or *C. procumbens*, suggested itself. However, the seedling stage of either of these two forms does not bear the remotest resemblance to that of *Capsella arachnoidea*. At the same time there was slight reason for believing that either *Capsella Heegeri* or *Capsella procumbens* ever had been grown in Ann Arbor.

During 1911 and the greater part of 1912, the problem rested here, no satisfactory explanation being found. But pedigree cultures were continued until, on the one hand, we succeeded in placing the plants in optimum surroundings for the production of climax leaves, and on the other began to distinguish between the various biotypes.

The Biotypes

As has been noted previously, it was possible to use two criteria for the classification of the rosets. Leaving out of consideration the rosets of the linear-leaved *arachnoidea*, it was found that after dividing the rosets according to the "broad" or "narrow" character of the earlier leaves (Fig. 3), it was possible to further subdivide each group on the basis of the marginal indentation of the leaves subsequently formed.

I. *The "Broad" Group.*—Here the first four or five leaves possess a blade which is approximately twice as long as broad. Up to this stage the margin remains entire. When the sixth leaf appears one ordinarily can begin to distinguish between two types. These are:

Type 1.—In this, the first of the two broad-leaved forms, the margin of the first eight leaves remains entire,

[10] Hus, H., "The Origin of Species in Nature," American Naturalist, **45**: 646, Nov., 1911.

showing at most a very slight crenation (Fig. 4). Usually the ninth leaf, though sometimes it is the eighth and sometimes the tenth, shows a more marked indentation, though seldom of a depth of more than 2 mm. on each side of the leaf and slightly below the middle. Subsequent leaves show an increase in the number and depth of the

FIG. 4. DISSECTION OF YOUNG ROSETS OF *C. . . . simplex* AND *C. . . . rhomboidea*, SHOWING THE "BROAD" CHARACTER OF THE EARLIER LEAVES AND THE DISTINCTIVE CHARACTER OF THE FIRST SINUS.

indentations, the maximum for both being reached in the climax leaves, which usually show five indentations reaching about midway from margin to midrib. In those of the earlier leaves which show a marked incision the lobes are obtuse. In the later leaves the lobes become acute. It may be stated as a general truth, that an increase in the depth of the sinus carries with it an increase in sharpness of the lobe. There is no secondary lobing, but sometimes the margin of the sinus shows a slight denticulation. While in the earlier leaves the sinuses separating the terminal lobe from the rest of the blade are the deepest,

the converse is true in the later leaves, where the sinuses separating the terminal lobe are the most shallow. I have identified this form with Shull's *simplex*.[11] My plants also agree fairly well with the illustration of ontogenetic succession of leaf forms in *Bursa* . . . *simplex*, shown by Shull.[12]

Type 2.—In the second of the two forms distinguished because of the greater relative width of their first leaves, the margin of the first five leaves remains entire, as in the case of those of type 1 (*simplex*). The sixth leaf, however, ordinarily shows a marked indentation, at least 3 mm. deep and slightly below the middle of the blade (Fig. 4). This indentation may appear in one margin or in both. The lower margin of the sinus ordinarily is at right angles to the midrib, the upper margin making an angle of 45 degrees with the midrib (Fig. 7, *b*). Even when it has become difficult to distinguish between types on the basis of relative width of the earlier roset leaves, it always is possible to distinguish between type 2 (*rhomboidea*) and type 4 (*Setchelliana* and *Treleaseana*), by means of the character of the sinus. In type 4, the lower margin of the sinus makes an angle of 45 degrees with the midrib, while the upper margin makes an angle of between 30 and 45 degrees with the midrib. Hence the first sinus in *C*. . . . *Setchelliana* and *C*. . . . *Treleaseana* is at least 90 degrees, while the first sinus in *rhomboidea* measures seldom more than 45 degrees and frequently less.

The seventh leaf of plants belonging to type 2 ordinarily shows two indentations on both sides of the leaf, dividing the blade into a lower portion, two central lobes and a terminal lobe. The depth of the incision amounts to about three-fourths of the width of the blade from midrib to margin.

It is possible to delay the appearance of the first indentations by transplanting from seedpan to flat either too early or too late. In such cases, the indentations appear in the seventh leaf only, or even later, and are rather

[11] *Loc. cit.*, 25, and Pl. 2, Fig. 2.

[12] Shull, G. H., "Verh. d. naturf. Ver. in Brünn," 49, Pl. 4, 1911.

shallow, reaching a depth of three-fourths of the width of the leaf from margin to midrib in the eighth, ninth or tenth leaf. However, once the indentations have made their appearance, the leaf next produced ordinarily shows two sinuses on both sides of the blade, usually the upper set, rarely the lower, being the deeper of the two, and almost reaching the midrib. The succeeding leaves show an increase in the number of lateral lobes from two to six. Since the incisions almost, if not quite, reach the midrib, both lateral lobes and the terminal lobes are well defined. Upon the lateral lobes secondary lobes appear, both on the distal and proximal margins. It is to be noted that only the climax leaves of well-grown specimens of the homozygotic form distinctly show the lobing of the proximal margin and this only on the middle lobes. The lobing of the primary lobes results in the setting off of a small terminal portion of each lateral lobe, which possesses a more or less rhomboidal form. This terminal lobe of the primary lobe can be observed to advantage only in the climax leaves of well-developed specimens.

I have no hesitation in identifying type 2 with Shull's *rhomboidea*.[13]

Capsella Bursa-pastoris simplex and *C. Bursa-pastoris rhomboidea*, described, respectively, as types 1 and 2, agree in having the first five or six leaves twice as long as broad, thus contrasting sharply with the plants to be described under types 3 and 4, which constitute the "narrow" group.

II. *The "Narrow" Group.*—In the plants belonging here, the first five or six leaves possess a blade which is from 2½ to 3 times as long as broad. Usually after the appearance of the seventh leaf, sometimes not until the appearance of the tenth leaf, it is possible, on the basis of marginal indentation, to separate the plants with "narrow" roset-leaves into two groups, designated respectively types 3 and 4.

Type 3.—Rosets of plants belonging to type 3 can not be distinguished from those of type 4, until after the

[13] Shull, Verh., Pl. 2; Biotypes, Pl. 1, Fig. 2.

seventh leaf has appeared (Fig. 5). It is to be noted that for the first six leaves of type 4, the ratio between mean length and width is 6:2, while for the corresponding leaves of type 3, the same ratio is 5:2. Once the seventh

FIG. 5. DISSECTION OF YOUNG ROSETS OF *x C. . . . Setchelli* AND *x C. . . . attenuata*, SHOWING THE "NARROW" CHARACTER OF THE EARLIER LEAVES AND THE DISTINCTIVE CHARACTER OF THE FIRST SINUS.

leaf has appeared, a distinction readily can be made, since in type 3, no sinuses appear, and the leaves, from the seventh to the tenth, might be mistaken for those of *simplex* (Fig. 5). Later leaves readily can be distinguished from those of *simplex*, by the pointed apex, the very shallow sinuses, ending in a sharp tooth, and by the fact that the greatest width of the blade lies above the middle, about one third the length from the tip (Fig. 6).

This form, which because of its morphological characters on the one hand, and its behavior in breeding on the other, can readily be distinguished from all others, I designate × *Capsella Bursa-pastoris attenuata.*

Type 4.—Not only do the first leaves of plants, belonging to this type, differ in relative width from the first leaves of plants of *rhomboidea* and *simplex*, but there also

is a difference in the apex of the leaf, the apices of leaves of this type, like those of type 3, being decidedly pointed, while those of types 1 and 2 are rounded.[14]

At the sixth or seventh leaf stage, the marginal indentations make their appearance, at first as slight crenations, then as long and shallow sinuses, and finally, in the eighth or ninth leaf, as a sinus on one or both sides of the midrib and about the middle of the blade (Fig. 5). The lower margin of the first sinus ordinarily makes an angle of 45 degrees with the midrib, while the upper margin makes an angle of from 30 to 45 degrees with the midrib. This renders the first sinus ordinarily greater than 90 degrees (Fig. 7, *a*). The depth of the first sinus is approximately one half the distance from margin to midrib. In subsequent leaves the depth increases, so that in the 11th leaf the sinuses almost reach the midrib. In *Treleasi*, one of the two forms, which together constitute type 4, the climax leaves show incisions to the midrib, and a well-marked terminal lobe, while in the other the sinuses are less deep but the terminal lobe still is well marked (Fig. 8). The number of sinuses increases in propor-

FIG. 6. LATER ROSET LEAVES OF *x C. . . . attenuata* AND *C. . . . simplex*.

[14] It is to be noted that in my cultures there appear, from time to time, plants of *rhomboidea* of which the leaves have sharply pointed lobes. What relation these plants bear to others classed with them under *rhomboidea*, I am at present unable to say.

tion to their depth. If the seventh leaf has one sinus in each margin, the eighth and ninth usually have two, the tenth and eleventh, three, and so on, until the mean of six is reached. As the lobes increase in number, they

FIG. 7. EARLY ROSET LEAVES OF *x C. . . . Setchelli* AND *C. . . . rhomboidea.*

FIG. 8. CLIMAX LEAVES OF *x C. . . . Setchelli* AND *x C. . . . Treleasi.*

not only become narrower but the sinuses do likewise. This is the result of a gradual increase in the angle between the lower margin of the sinus and the midrib. In the eighth leaf the lower margin forms an angle of about 90 degrees with the midrib, causing the formation of a primary lobe, triangular in shape and with an upper angle of about 45 degrees, instead of the 90-degree angle found in the first lobe. In older leaves the angle between lower margin of sinus and midrib may increase to 110 or even 120 degrees. The climax leaves therefore get to resemble more and more those of *rhomboidea,* especially since the distal margin of the sinus, from the tenth leaf on, exhibits a number of denticulations which, in older leaves, especially of one of the forms (*Treleaseana*), tend to become incisions, so that secondary lobes are

formed. However, the end of the lobes of early leaves of type 4 always are sharply pointed (Fig. 9), while the lobes of early leaves of *rhomboidea* are ordinarily rounded at the ends (Fig. 4).

Fig. 9. Upper Row: 3 Sets of Leaves from as Many Plants of *x C. . . . Treleasi.* Lower Row: 4 Sets of Leaves from as Many Plants of *x C. . . . Setchelli.*

From a morphological point of view these leaves are entirely different from any form described by Shull, the differences being most marked and very readily recognized once our attention has been called to them. But it is especially the behavior of the plants on breeding which leads me to recognize them as most distinct hybrid forms and which I have designated × *Capsella Bursa-pastoris Setchelliana* in honor of Professor William Albert Setchell, and × *Capsella Bursa-pastoris Treleaseana,* in honor of Professor William Trelease.

Type 5.—Capsella Bursa-pastoris arachnoidea. This form, which readily is recognized from the first by its linear leaves, does not require an elaborate description at present, since it will be discussed in detail later. It has been illustrated in Figs. 1, 2 and 3.

The above descriptions apply only to plants grown under fairly uniform conditions, in a light soil in a greenhouse, and treated in such a manner as to offer the plant the most favorable conditions for development. By leaving the plants too long in the flats, so that crowding results, by keeping them too moist and warm, etc., it is possible to produce abnormal climax leaves in which the typical differences can be recognized with difficulty only. By leaving plants too long in the seedpans, by keeping them too dry, it may be brought about that plants flower without having produced climax leaves. There will be doubtless many who, because of this, will refuse recognition to the segregates just described. "Quæcunque dixi, si placuerint, dictavit auditor." Fortunately, the differences of behavior on breeding are such, we must recognize their distinct genotypic constitution.

Genotypic Constitutions

Shull, in the papers above quoted, made one of the most important of recent contributions to science, since he determined with exactitude the relations existing between some of the lesser forms which, because of their alleged constancy or inconstancy, have been a bone of contention since the days of Jacquin. Making extensive cultures of *Capsella,* Shull was able to distinguish four forms (Fig. 10), to wit, *heteris,* with leaves divided to the midrib, with

FIG. 10. CLIMAX LEAVES OF *C. . . . heteris, C. . . . tenuis, C. . . . rhomboidea* AND *C. . . . simplex.*

elongated primary lobes, a marked secondary lobe, in the distal axil of the primary lobe and a well-marked terminal lobe; *rhomboidea,* with leaves divided to the midrib, with an unelongated primary lobe, with an incision in the distal margin setting off a secondary lobe and a corresponding incision on the proximal margin of the primary lobe, setting off, in well-grown specimens, a terminal portion of each lateral lobe, generally of rhomboidal form; *tenuis,* with the elongated primary lobe of *heteris*, but with a sinus which usually does not reach the midrib, terminal lobe clear cut; *simplex,* with lateral lobes obtuse, never attenuated, the incisions being shallow and never reaching the midrib.

Shull recognized here the presence and absence of two factors, one (A) responsible for the sharp primary lobe of *heteris* and the attenuation of the lobes in *tenuis,* while the other (B) is responsible for the division of the leaf to the midrib, the definite terminal lobe and the secondary lobes. On this basis Shull was able to represent the biotypes by conventional Mendelian symbols, thus: *heteris, AB; rhomboidea, aB; tenuis, Ab; simplex, ab.*

That this conventional presentation gives us a reliable working basis, my experiments have shown most satisfactorily. With the aid of these symbols I have been able to solve the origin of *Capsella arachnoidea,* the experiments showing that, without question, forms presenting the spider-like appearance of the rosets typical of this plant are of hybrid origin.

The Zygotic Constitution of 4,108.6

The problem to be solved was that of the zygotic constitution of the original parent, the plant which in my notes is recorded as 4,108.6. Among its offspring neither *heteris* nor *tenuis* made their appearance, while both *rhomboidea* (aB) and *simplex* (ab) were met with. Hence the parent was homozygotic for (a), but heterozygotic for (B). Therefore, its zygotic constitution, in part, must have been *aaBb.*

Besides *rhomboidea* and *simplex* there appeared two

forms, referred to as types 3 and 4, the latter being capable of further subdivision. Neither of these was described by Shull. At least one difference between *rhomboidea* and *simplex,* on the one hand, and types 3 and 4, on the other, could be noted at once, *i. e.,* the relative width of the leaf. As has been shown above, the former have their first leaves twice as long as broad, the latter three times as long as broad. The idea suggested itself that there might exist a factor which determined these characters. Since the original parent belonged to type 4, the narrow character of the earlier leaves must be dominant over the broad character. Also, since the original parent produced both "narrow" and "broad" types, it must have been heterozygotic for this character. Using (N) to indicate the gene, we get for the zygotic construction of the parent plant *aaBbNn.*

	aBN	*aBn*	*abN*	*abn*
aBN	1 *aBN* *aBN*	2 *aBn* *aBN*	3 *abN* *aBN*	4 *abn* *aBN*
aBn	5 *aBN* *aBn*	6 *aBn* *aBn*	7 *abN* *aBn*	8 *abn* *aBn*
abN	9 *aBN* *abN*	10 *aBn* *abN*	11 *abN* *abN*	12 *abn* *abN*
abn	13 *aBN* *abn*	14 *aBn* *abn*	15 *abN* *abn*	16 *abn* *abn*

FIG. 11. DIAGRAM TO ILLUSTRATE THE NATURE OF THE OFFSPRING OF *x C. . . . Setchelli* (*aaBbNn*).

Since self-fertilization is the rule in *Capsella,* it was an easy matter to test the validity of the theory. A form *aaBbNn,* one with unelongated primary lobes, sinuses reaching the midrib and with early leaves of a "narrow" type should yield, on self-fertilization, the following combinations: 1.*bbnn* (square 16), a plant of which, according to our definition, the earlier roset leaves should be

broad and of which the later leaves shall lack incisions reaching to the midrib, a plant, in short, which should have all the characteristics of Shull's *simplex*. Furthermore, on being selfed, it should yield a uniform offspring, in all respects resembling the parent.

Such plants actually were encountered. Of the plants grown to maturity, twelve were selected as seed-bearers. All bore the *simplex* character. Ten of these plants were selected from among the first generation of plants of the supposed zygotic constitution *BbNn*, while one parent (yielding No. 25,712) was derived from a plant bearing the *simplex* character and another (yielding No. 31,112) was derived from a plant which was shown to have the zygotic constitution *bbNn*.

TABLE I

EVIDENCE OF HOMOZYGOTIC CHARACTER OF *Simplex* (*bbnn*)

Index Number	Number of Plants		Index Number of Parent	Character of Parent	Character of Grand-parent
25,712	78	*G*[15]	8,112*BR*12*P*9	*bbnn*	*bbnn*
25,912	22	*G*	8,212*BR*3*P*1	*bbnn*	*BbNn*
26,312	42	*G*	8,212*CR*5*P*1	*bbnn*	*BbNn*
26,512	187	*G*	8,212*FR*3*P*3	*bbnn*	*BbNn*
26,712	180	*G*	8,212*HR*7*P*7	*bbnn*	*BbNn*
30,012	276	*O*	8,212*CR*5*P*1	*bbnn*	*BbNn*
30,112	108	*O*	8,212*HR*2*P*6	*bbnn*	*BbNn*
30,212	60	*O*	8,212*GR*6*P*8	*bbnn*	*BbNn*
30,312	162	*G*	8,212*GR*6*P*8	*bbnn*	*BbNn*
30,712	27	*O*	8,212*HR*3*P*6	*bbnn*	*BbNn*
31,112	50	*O*	26,012*AR*7*P*6	*bbnn*	*bbNn*
3,113	207	*O*	26,912*BR*1*P*3	*bbnn*	*BbNn*
	1,399				

This table offers an excellent illustration of the small danger of an accidental cross, even if the plants are not guarded, always, of course, when the proper precautions, indicated above, are taken. Numbers 26,312 and 30,012, as well as numbers 30,212 and 30,312, respectively, offer instances of uniform inheritance in plants possessing recessive characters only and of which the parents in the one case were left unguarded, in the other caged. Had

[15] In this column "*G*" indicates that the parent plant was guarded, "*O*" that the plant was open-fertilized. In other tables the same abbreviation will be used.

crossing taken place in the case of the unguarded flowers, this would, because of the purely recessive characters possessed by *simplex*, have become apparent at once. In all cases the parents were checked by means of herbarium specimens or photographs, or both.

2. *bbNN* (square 11). According to our hypothesis, a plant of this zygotic construction should have the earlier roset leaves narrow and the climax leaves should lack incisions to the midrib. It also should breed true. A plant fulfilling these conditions has not been encountered, or rather, its recognition was delayed until the offspring of the corresponding heterozygote *bbNn* could be observed. As will be shown, the zygotic combination *bbNN* yields a plant with the external characteristics of *arachnoidea*.

3. *bbNn* (squares 12 and 15). A plant of this zygotic constitution should have narrow early leaves and the climax leaves should lack incisions to the midrib. On self-fertilization it should yield 25 per cent. *bbNN*, 50 per cent. *bbNn* and 25 per cent. *bbnn*.

bN *bN*	*bn* *bN*
bN *bn*	*bn* *bn*

Several plants were found which fulfilled the requirements as to leaf characters. Such plants, on being selfed, yielded approximately 25 per cent. *simplex*, which we know to have the zygotic constitution *bbnn*, while about 50 per cent. bore the parental characters, supposedly represented by *bbNn*. The remaining 25 per cent. clearly belonged to the type *arachnoidea*. In all, 12 plants were selected as seed-bearers, some being guarded, others remaining uncaged. The results are given in Table II.

The totals closely approximate the Mendelian ratio, yielding, respectively, *bbNN* 24 per cent., *bbNn* 49 per cent. and *bbnn* 27 per cent. Having established the identity of *bbnn* (*simplex*) and *bbNn* (*attenuata*), we are forced to recognize *bbNN* as the zygotic construction of *arachnoidea*. It would be a comparatively easy matter to test

this directly, provided the form *arachnoidea* produced seed. Though I have grown several hundreds of these plants, I have obtained in all but eight seeds, and these as the result of hybridization. Hence the test must be made indirectly through crossing of forms yielding the desired gametic combinations.

TABLE II

EVIDENCE OF HETEROZYGOTIC CHARACTER OF *attenuata* (*bbNn*)

Index Number	Number of Plants						Index Number of Parent	Char. of Parent	G or O	Char. of Grand-parent
	bbNN		*bbNn*		*bbnn*					
	Found	Expected	Found	Expected	Found	Expected				
26,012	19	25.50	56	51.00	27	25.50	8,212*BR*5*P*1	*bbNn*	*G*	*BbNn*
26,412	8	7.50	14	15.00	8	7.50	8,212*DR*10*P*8	*bbNn*	*G*	*BbNn*
31,212	16	14.75	27	29.50	16	14.75	26,012*AR*2*P*1	*bbNn*	*O*	*bbNn*
31,312	22	15.00	19	30.00	19	15.00	26,012*AR*1*P*2	*bbNn*	*O*	*bbNn*
31,412	10	14.25	25	28.50	22	14.25	26,012*AR*1*P*3	*bbNn*	*O*	*bbNn*
31,512	24	25.50	47	51.00	31	25.50	26,012*AR*1*P*4	*bbNn*	*O*	*bbNn*
31,612	2	2.50	4	5.00	4	2.50	26,012*AR*6*P*6	*bbNn*	*O*	*bbNn*
31,812	26	28.25	54	56.50	33	28.25	26,012*BR*1*P*3	*bbNn*	*O*	*bbNn*
31,912	11	16.50	40	33.00	15	16.50	26,012*BR*1*P*6	*bbNn*	*O*	*bbNn*
3,213	61	64.25	130	128.50	66	64.25	26,912*DR*2*P*4	*bbNn*	*O*	*BbNn*
3,313	70	61.50	117	123.00	59	61.50	26,912*ER*6*P*6	*bbNn*	*O*	*BbNn*
3,513	27	35.50	71	71.00	34	35.50	26,912*FR*6*P*4	*bbNn*	*O*	*BbNn*
Total .	296	308.50	604	617.00	334	308.50				

Of the twelve parent plants concerned in the above experiment, five were selected from among the first generation of a plant having the supposed zygotic constitution *BbNn*, while seven were the direct offspring of No. 26,012, which had been shown to yield the three forms, *arachnoidea, attenuata* and *simplex*, as indicated in Table II.

The *simplex*, obtained by selfing a plant of *bbNn*, breeds true, as indicated in Table I, No. 31,112, a *simplex*, yielding a uniform *simplex* offspring, consisting of 50 individuals.

4. *BBnn* (square 6). A plant of this supposed zygotic constitution should resemble, in all respects, Shull's *rhomboidea*, the earliest roset leaves being broad, and the incisions of the climax leaves reaching the midrib. It should breed true. Five lots, involving four parents, were grown. Again it was shown, in the case of No. 26,812 and

No. 30,612, that the fact that plants are left unguarded does not affect results. The parents, in all cases, were selected from among the first generation of plants having the supposed zygotic constitution *BbNn*. The results are given in Table III.

TABLE III

EVIDENCE OF HOMOZYGOTIC CHARACTER OF *rhomboidea* (*BBnn*)

Index Number	No. of Plants	Index Number of Parent	Char. of Parent	*G* or *O*
25,812	20	8,212*BR*1*P*6	*BBnn*	*G*
26,812	80	8,412*BR*3*P*2	*BBnn*	*G*
27,012	6	8,412*ER*10*P*6	*BBnn*	*G*
27,112	210	8,412*ER*13*P*12	*BBnn*	*G*
30,612	96	8,412*BR*3*P*2	*BBnn*	*O*

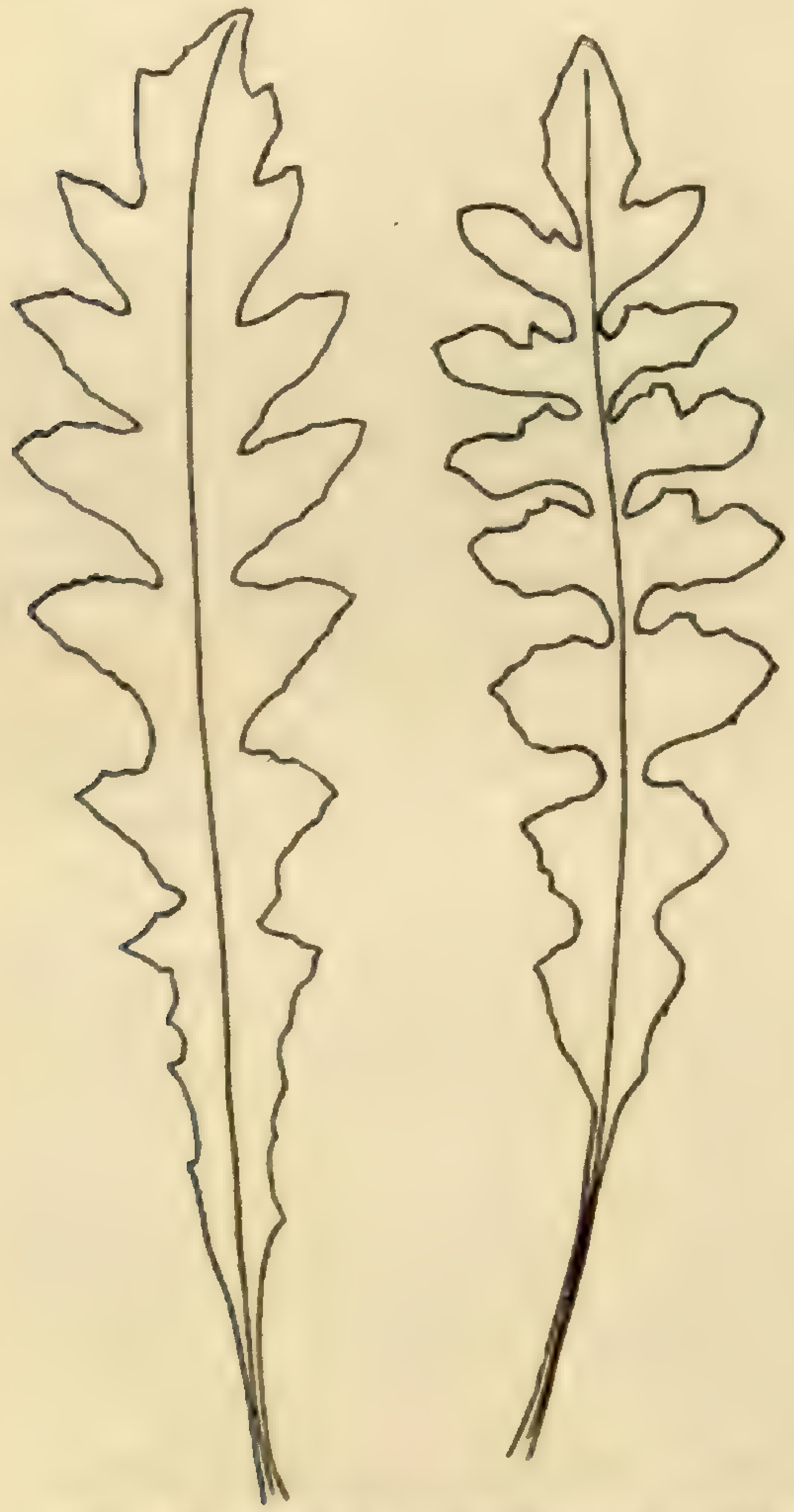

FIG. 12. CLIMAX LEAVES OF A HETEROZYGOTIC *C. . . . rhomboidea* AND OF A HOMOZYGOTIC *C. . . . rhomboidea*. . .

In all cases the offspring was uniformily of the *rhomboidea* character.

Bn *Bn*	*Bn* *bn*
Bn *bn*	*bn* *bn*

5. *Bbnn* (squares 8 and 14). Plants of this zygotic constitution should resemble those of the preceding group, but on being selfed should yield 25 per cent. homozygotic *rhomboidea* (*BBnn*), 50 per cent. heterozygotic *rhomboidea* (*Bbnn*) and 25 per cent. *simplex* (*bbnn*).

These three forms were found to constitute the offspring of a single plant, 8,212*HR*1*P*3, itself an offspring of a plant of the supposed zygotic constitution *BbNn*. This plant, from

[16] Bursa . . . 39.

the first, was classified as a *rhomboidea*. At the present time, a photograph of the young roset confirms this classification. But two climax leaves, which, in the earlier part of these experiments, were deemed sufficient, show that the sinuses do not quite reach the midrib (Fig. 12). Unfortunately, Shull, in the description of his No. 054.28,[16] does not mention this point, though he does point out that "the later rosette-leaves had some of the secondary lobes acutish, but not elongated." In the older climax leaves, even of a homozygous *rhomboidea,* I find that the secondary lobes disappear. Shull, in the description just referred to, is so specific as to the typical *rhomboidea* character of the heterozygote that I have hesitated to classify the heterozygotes and the homozygotes. But the homozygotic *rhomboidea,* obtained as the extracted recessive of a selfed plant of the supposed zygotic constitution *BBNn,* always has sinuses which reach the midrib. In other combinations, also, one can distinguish between *BB* and *Bb* by the relative depth of the sinus. For the present, then, we will rely upon this character. In the case under discussion (26,612, the offspring of 8,212*HR*1*P*3, guarded) there were among the 39 plants 6 which clearly were *simplex,* the heterozygotic *rhomboidea* was represented by 22 individuals, and the homozygotic *rhomboidea* by 11 individuals, the calculated ratio being 9.75 : 19.50 : 9.75. The percentage of *simplex* is far too low, 15.4 per cent., instead of 25 per cent., but, considering the small number of individuals concerned, the total outcome is fairly satisfactory. It is almost unnecessary to add that in this, as in other cases, the offspring of the various plants is being tested as fast as time and facilities permit.

Type 4.—Having shown the presumable correctness of our supposition as to the zygotic constitution of the initial plant (*BbNn*), as far as the presence, appearance and behavior on breeding of *simplex, rhomboidea* and *attenuata* are concerned, there remains to identify the major group of combinations which, in a simple di-polyhybrid, constitutes

nine sixteenths of the total offspring and may be uniform in appearance, the constituents being separable only by breeding, "eine heillose Arbeit," as Baur has it. Fortunately, in this case, it is possible to distinguish readily between the various combinations.

One of the combinations, *BBNN* (square 1), should breed true, being homozygotic for both characters concerned. We would expect such a plant to have narrow first leaves and climax leaves with incisions to the midrib. Thus far I have not encountered such a plant, something which at one time led me to consider the possibility of gametic repulsion, in this instance the gamete *BN* being incapable of existence. This supposition seemed the more plausible since the two genes *B* and *N* well might be supposed to be antagonistic, the one being responsible for an incision of the leaf to the midrib, the other tending to make the leaf, especially the earlier leaves, narrow. Were this assumption correct, none of the zygotic combinations found in squares 1, 2 and 5, 3 and 9, and 4 and 13, would be formed, though we would expect the same combination as occurs in squares 4 and 13 to make its appearance as the result of the fusion of the gametes *bN* and *Bn* (squares 7 and 10).

Were this supposition correct, we should have a case similar to that of the sweet pea "Purple Invincible," and we could not expect the gamete (*bn*) to be formed. Since, however, *simplex* (*bbnn*) appears in our cultures, this theory must be rejected. Recently also, in culture No. 30,412, an instance was found in which the guarded parent, supposedly of type 4, yielded, not *simplex, rhomboidea, attenuata, arachnoidea* as well as the parental type, but only *arachnoidea, rhomboidea* and the parental type, and in proportions closely approximating a ratio 1:1:2.

A plant which yielded 25 per cent. *rhomboidea* and no *simplex,* must have been homozygotic for *B,* and since it yielded also 50 per cent. of type 4, must have been heterozygotic for *N,* its zygotic constitution therefore being *BBNn.* Such a plant, on self-fertilization, should yield 25 per cent. *rhomboidea.* Provided the homozygote and

the heterozygote have the same appearance, the remaining 75 per cent. should resemble the parent (Fig. 9, *b*).

BN *BN*	*Bn* *BN*
BN *Bn*	*Bn* *Bn*

But in one case (30,412), the parent being 8,412*BR9P9*, and open fertilized, the offspring consisted of 26.3 per cent. *rhomboidea,* 46.2 per cent. of the parental type and 27.5 per cent. *arachnoidea.* If our supposition as to the zygotic constitution of the parent is correct, then the zygotic constitution of the *arachnoidea* in this offspring must be *BBNN*. In the case of a selfed *attenuata,* we found that approximately 25 per cent. of the offspring was composed of *arachnoidea* of the probable zygotic constitution *bbNN*. Is it possible that any *Capsella,* homozygotic for *N,* would have the appearance of *arachnoidea?* This seems more than probable, and other evidence, to be adduced later, appears to support this view. The history of the *BBNn* is as follows:

During 1912 I grew No. 8,412 from seeds of a plant which resembled the grandparent 4,108.6. It was composed of 1,079 individuals, among which various types, such as "broad," "narrow" and "linear," could be recognized. Not all plants were thus classified, a fourth group of "intermediates" being formed, indicating that some of the plants, while in certain respects resembling *simplex* and especially *rhomboidea* (deep lobing, secondary lobes), in other characters more closely approximated the "narrows," since their early leaves had been noted as "narrow." In the light of recent experience, it is easy to see why the distinction was made, though at the time the conception of the differences was most hazy. Several of these "intermediates" were grown, and of these a single one yielded the seed for the next generation. This plant had been permitted to flower unguarded, but after a number of capsules had developed on the main stalk, this was decapitated and the sideshoots were allowed to de-

velop. At this time the entire plant was caged. Subsequently the seeds of the open fertilized and of the guarded flowers were sown separately, with the following results:

	30,412. Open Fertilized			30,512. Guarded		
	Per Cent.	Plants		Per Cent.	Plants	
		Found	Expected		Found	Expected
Arachnoidea	27.5	40	36.25	21.15	52	61.50
"Narrow"	46.2	67	72.50	36.15	89	123
Rhomboidea	26.3	38	36.25	42.70	105	61.50

The figures are given separately to again call attention to the fact that open fertilization is no hindrance to pedigree work in *Capsella*. Since the seeds came from the same parent, we may add the results, which gives us *arachnoidea* 23.50 per cent., "narrow" 40 per cent. and *rhomboidea* 36.50 per cent. The fact that the percentage for "narrow" is too low and that for *rhomboidea* too high, while the percentage for *arachnoidea* is within the limits of probable error, is probably due to errors in classification, since greater weight was laid upon lobing of the adult leaves than upon comparative width of the earlier ones. The value of this culture lay chiefly in its suggestion of a zygotic combination *BBNn,* which prior to that time, on account of the gametic repulsion theory, was not supposed to exist. In consequence, a number of cultures were made, with the following result:

TABLE IV

EVIDENCE OF HETEROZYGOTIC CHARACTER OF *Treleaseana* (*BBNn*)

Index No.	Number of Plants						Index No. of Parent	Char. of Parent	O or G	Char. of Grand-parent
	BBNN		*BBNn*		*BBnn*					
	Found	Expected	Found	Expected	Found	Expected				
3,813	38	30	56	60	26	30	30,412*AR*2*P*6	*BBNn*	*O*	*BBNn*
3,913	36	44.75	87	89.50	56	44.75	30,412*AR*4*P*3	*BBNn*	*O*	*BBNn*
4,013	14	15.25	28	30.50	19	15.25	30,412*AR*6*P*3	*BBNn*	*G*	*BBNn*
4,213	15	28.50	65	57	34	28.50	30,412*BR*2*P*6	*BBNn*	*O*	*BBNn*
4,313	33	33	62	66	37	33	30,412*BR*6*P*5	*BBNn*	*O*	*BBNn*
4,413	37	45.25	102	90.50	42	45.25	30,412*BR*9*P*2	*BBNn*	*O*	*BBNn*
Total	173	196.75	400	393.50	214	196.75				

The "narrows" in question, then, fulfilled our expectation on the basis of a zygotic constitution *BBNn*. In some cases the percentages are too high, in others too low. The total yields fairly satisfactory results, to wit: *BBNN* 22 per cent., *BBNn* 51 per cent. and *BBnn* 27 per cent. Two tests of the extracted recessive, a homozygotic *rhomboidea,* were made. The cultures, No. 3,713, from a guarded *rhomboidea* (30,412*AR*2*P*3) and No. 4,113, from an unguarded *rhomboidea* (30,412*AR*8*P*3), both derived from plants of the supposed zygotic constitution *BBNn,* yielded, respectively, 54 and 207 plants, all of which bore the typical *rhomboidea* characters.

In the cultures just tabulated, the plants of the supposed zygotic constitution *BBNn* resembled the parent in all respects. The form *arachnoidea,* in this case, must have the zygotic formula *BBNN*. Unfortunately, in this case also, it proved unfertile.

A better acquaintance with plants of the zygotic constitution *BBNn* led us to formulate certain differences between them and our original "narrow." Plants of the *BBNn* character, readily can be segregated from those of the *BbNn* character by somewhat narrower primary lobes, split to the midrib and the development, in climax leaves of well-grown specimens, of a secondary lobe, not pronounced but recognizable (Figs. 8, 9).

On the basis of these morphological differences, as well as because of the behavior of the plant on breeding, I propose to segregate it from type 4 under the name × *Capsella Bursa-pastoris Treleaseana*. This form is homozygotic for *B,* while *Setchelliana* is heterozygotic for *B*. Both are heterozygotic for *N*. They may be expected to look alike during the early stages. Later they show a difference, since the form containing *Bb* does not develop sinuses as deep as the form containing *BB*. The form *Treleaseana,* when young, can readily be distinguished from a heterozygotic *rhomboidea* (*Bbnn*) by the relative width of the early leaves; later such a distinction is difficult (Figs. 4, 5, 7). If any distinction at all is to be made, it should be made on the basis of the rounding

of the lobes, those of *Treleaseana* being sharp, those of the heterozygotic *rhomboidea* rounded.

I am fully aware that in thus naming genotypes, I am departing from all rules laid down by systematists. But a rule is useful only as long as it serves a purpose. For the geneticist, the rules of systematists are of small value. Subspecies, variety, form, are, after all, but very general terms, almost incapable of definition because of too frequent abuse. But once we have determined the zygotic constitution of any plant, we have placed ourselves on a firmer basis. Behavior in breeding is the proper criterion. And while I recognize that this, for systematic purposes, is impracticable, at the same time I assert the right to use a trinomial for any organism of known zygotic constitution, this being, at the present time at least, the easiest way of designating any particular form. Some day we shall have formulas, corresponding to those of chemistry, to designate the lesser forms.

The increase in the number of named forms, a necessary consequence, need cause no alarm, since they concern only him who occupies himself with one species exclusively. But we must go even further than this. Squarely facing the issue, we find ourselves placed in a position which necessitates the naming of heterozygotes. Obviously, numerous objections could be urged. But since it has been shown, on the one hand, that certain forms can exist only in a heterozygous form (Baur's *Antirrhinum*) and, on the other, that not only the difference between the homozygote and the heterozygote is as great as that between many of our "systematic" species (for instance, *attenuata, bbNn,* and *arachnoidea, bbNN*), but that a homozygotic condition for a single gene gives the same result, whatever the condition of the other known genes, at least as thus far determined (*arachnoidea* occurs as *aaBBNN, aaBbNN* and *aabbNN*), the advantage of naming all forms of different zygotic constitution must be granted.

Thus far we have not encountered a plant of the zygotic constitution *BbNN,* at least as far as can be judged from

breeding experiments. On being selfed such a plant should yield:

BN *BN*	*bN* *BN*
BN *bN*	*bN* *bN*

It has been shown that plants of the zygotic constitution *BBNN* and *bbNN* exhibit the *arachnoidea* type. At least 50 per cent. of the offspring then should show this character. But if the suggestion made above is the correct one, *i. e.*, that all plants homozygotic for *N* exhibit the *arachnoidea* type, then the parent and its entire offspring should bear this character. The unfortunate infertility of *arachnoidea* prevents us from submitting this hypothesis to direct experimental proof. But there exist indirect means for establishing the probable truth of our contention. In the first place, we may cross two plants, the identity of which can be established beyond doubt, to wit, *attenuata* (*bbNn*) and *Treleaseana* (*BBNn*). Such a cross would yield:

BN *bN*	*Bn* *bN*
BN *bn*	*Bn* *bn*

Of these, we would recognize *Bbnn* because of its *rhomboidea* character, 50 per cent. would be recognized as *Setchelliana* (*BbNn*), while the remainder, if our surmise is correct, would consist of *arachnoidea*. Experiments to determine this are under way. At the present we have another, though by far less accurate, means of testing our hypothesis. If the combination *NN* always results in a form *arachnoidea*, the offspring of a plant of the zygotic constitution *BbNn* would be composed of:

4 *Setchelliana* (*BbNn*),
2 *Treleaseana* (*BBNn*),
2 *attenuata* (*bbNn*),
4 *arachnoidea* (1 *BBNN*, 2 *BbNN*, 1 *bbNN*),

3 *rhomboidea* (1 *BBnn*, 2 *Bbnn*),
1 *simplex* (*bbnn*).

Since *BbNn, BBNn* and *bbNn,* in the earlier experiments, might have been confounded in the later stages, and since there is little doubt as to the earlier stages, these three forms have been combined in Table V.

TABLE V

RESULTS FROM SELECTED *Setchelliana* (*BbNn*)

Index No.	"Narrow"		*arachnoidea*		*rhomboidea*		*simplex*	
	Found	Expected	Found	Expected	Found	Expected	Found	Expected
26,912	134	157.6	94	78.8	68	59.1	19	19.7
3,613	94	89	45	45	33	33.75	8	11.25

This, especially in the case of No. 3,613, is a fairly close approximation to what we might expect. When in No. 3,613 we attempt to distinguish between *Setchelliana, Treleaseana* and *attenuata,* we get the following numbers, the expected numbers following in parentheses: *BbNn* 39(45), *BBNn* 21(22.50), *bbNn* 34(22.50), the last number being far too high. When the experiments were begun, we distinguished only between "narrow," "broad" and "linear." To-day we know that the "narrows" include *Treleaseana, Setchelliana* and *attenuata,* that the "broads" include *rhomboidea* and *simplex,* while the linears are identical with *arachnoidea.* In this light it is of interest to go back to the first generation of 1910. Our data yield the figures given in Table VI.

TABLE VI

Index No.	"Narrow"		"Linear"		"Broad"	
	Found	Expected	Found	Expected	Found	Expected
7,911	34	30.50	9	15.25	18	15.25
8,111	27	35.50	16	17.75	28	17.75
8,311	66	61	32	30.50	24	30.50
8,711	27	27	15	13.50	14	13.50
8,811	49	46.50	20	23.25	24	23.25
9,011	4	7.50	4	3.75	7	3.75
9,511	93	76	32	38	27	38
9,611	28	23.50	5	11.75	14	11.75
Total	328	308.50	133	154.25	156	154.25
Per cent	53.2	50	21.5	25	25.3	25

It must be granted that the approximation is fairly close, and that, taken in consideration with the others, it offers ample support for the correctness of the diagnosis of the zygotic constitution of the original plant. It at least offers a working basis. One would be tempted to accept it as a final solution were it not for the fortunate appearance of a plant which does not fit into our scheme and which, provisionally, has been named *Capsella Bursa-pastoris orbicularis.*

Capsella Bursa-pastoris orbicularis

This form differs from any other plant encountered in my cultures. While in a general manner resembling *simplex,* it differs in being more robust, having larger flowers (though not as large as those of *C. grandiflora*), and in having orbicular first leaves (Fig. 13). All leaves are covered with stout hairs. It is a plant which tempts us to draw a parallel between it and *Œnothera gigas,* a name which I have not used for the sake of avoiding an implied comparison.

Fig. 13. Seedlings of *C. orbicularis.*

The first plant of this type appeared in a culture of *attenuata* (26,012*BR*3*P*5) and was of sufficiently striking appearance, though but four or five leaves had developed, to call for a special note and a photograph. Later the plant was potted and finally seed was gathered from the unguarded plant. From this seed four seedlings were obtained. At least three of them closely resembled the parent, the fourth having somewhat narrower leaves. Later the differences between these plants and those of *simplex* became more apparent (Fig. 14). Those of my students to whom the differences have been pointed out have not the slightest difficulty in distinguishing between the two forms. It is hoped that later, when by means of prolonged cultures I shall have made myself more familiar with this form, it may be made the subject of a distinct paper where histological and cytological studies will find

a place. One would be inclined to look upon *orbicularis* as a mutation. But the fact that at first we classed *arachnoidea* as such, later to prove it of hybrid origin,[17]

FIG. 14. FOUR SEEDLINGS OF *C. . . . orbicularis* AND (THE LOWER) TWO SEEDLINGS OF *C. . . . simplex.*

would tend to make us cautious, and lead us to attempt to find a solution for the origin of *orbicularis* in the dissociation or combination of certain "units." While I should not care to go quite as far as M. Heribert Nilson[18] "das ganze Mutations phänomen durfte unter einen gemeinsamen Gesichtspunkte: der Mendelschen Neukombination eingeordnet werden können," yet it is probable that here the majority of alleged mutations may be classed.

[17] Baur's (Vererbungslehre, 189) narrow-leaved *Melandrium album* is perhaps susceptible of the same explanation.

[18] *Zeitschr. f. ind. Abst. u. Bererb.*, 8: 89, 1912.

An examination of the herbarium material placed at my disposal reveals the fact that plants, apparently identical with *C. orbicularis,* occur in Europe. In the Engelmann herbarium of the Missouri Botanical Garden are two sheets (No. 3,661 and 3,664) containing specimens which undoubtedly must be classed here. The latter sheet bears the label: *Thlaspi Bursa-pastoris humile.* Heidelberg. April 1828.

A culture of *Capsella,* derived from seed of a single plant, unfortunately not preserved, escaped from cultivation in the Experiment Garden, and consisting of 182 individuals (Ehlers, No. 4,813), appears to be composed entirely of *orbicularis.* And while I have never encountered the plant in nature, these two facts lead us to another possible explanation. Perhaps the appearance of *orbicularis* in the original culture was due to an accidental admixture, such as is almost impossible to guard against when experimental plants are grown in a greenhouse used for a variety of purposes.

The exact relation which *orbicularis* bears to the other types of *Capsella* here described can, of course, be determined only after a series of experiments has been carried out. However, the delay in the completion of the manuscript, caused by the unfortunate destruction, by fire, of the botanical laboratories of the University of Michigan, enables me to add that a third generation of *orbicularis,* the parent being No. 32,012*R*1*P*3, shows at least two and possibly three types, of which one is especially interesting in having rather narrow leaves, at least as compared with those of typical *orbicularis.* The contrast between the two forms is increased by the fact that in the narrow-leaved form the foliage is entirely glabrous, while in the typical *orbicularis* the leaves are covered with numerous stiff, almost bristle-like, hairs.

× Capsella Bursa-pastoris arachnoidea

By this name is designated the linear-leaved form, the appearance of which induced us to undertake the cultivation of *Capsella Bursa-pastoris Setchelliana.*

Fig. 15. Rosets Illustrating the Two Types

Already the leaves which immediately follow the cotyledons serve to distinguish plants of this type from all others. At the ten-leaf stage even the casual observer is able to segregate them at once from the other rosets. The leaves are acicular and the cotyledons far larger than those of the seedlings of the other forms. The greater size of the cotyledons may be attributed to the insufficiency of the subsequent leaves.

If one removes the terminal bud of seedlings of *Atriplex hortensis* or one of its color varieties, it will be found that the cotyledons increase in length far beyond normal, sometimes reaching a length of 8 cm. Under favorable conditions the leaves of × *C. arachnoidea* may reach a length of 100 mm., with a greatest width of 6 mm. (Fig. 16). The stem ordinarily is weak, having a diameter of only 1 mm. It may reach a length of 30 cm. (Fig. 17).

THUS FAR RECOGNIZED IN *C. . . . orbicularis.*

The flowers are small, the petals especially so. The anthers shrivel up early and as a rule are devoid of pollen grains. Occasionally a few can be demonstrated. The ovary, though small, contains what appear to be ovules capable of being fertilized. Thus far I have collected eight seeds contained in 6 capsules on unguarded plants of *arachnoidea* (Fig. 18). Two of these germinated, the one yielding a plant which looks like *simplex,* though having a large amount of red coloring matter in the petioles, while the other is an *arachnoidea.* Attempts to artificially fertilize *arachnoidea* have failed absolutely.

As has been shown above, one may distinguish, on the basis of genotypic constitution, three forms of *arachnoidea,* viz.: *BBNN, BbNN* and *bbNN.* Externally no

differences can be noted. A single exception perhaps may be made to this statement. It had been noted that specimens of *arachnoidea* frequently showed fasciation. This fasciation seems most marked in plants of the zygotic constitution *BBNN* (Figs. 19, 20, 21).

Fig. 16. Roset of *x C. . . . arachnoidea.*

While it is hoped that later a more extended report may be made upon this plant, at present it may be stated that there exists the probability that it may throw some light upon the nature of fasciations. In earlier publications[19] I have brought together some of the known facts bearing upon this teratological character. Though a large por-

[19] "Fasciation in *Oxalis crenata* and Experimental Production of Fasciations," *Rep. Mo. Bot. Gard.*, **17**: 147, 1906; "Fasciations of Known Causation," American Naturalist, **42**: 81, 1908; "Inheritance of Fasciation in *Zea Mays*," *The Plant World*, **14**: 1911; "The Origin of Species in Nature," American Naturalist, **45**: 641, 1911; "Frondescence and Fasciation," *Plant World*, **14**: 1911; "Fasciation in *Oxalis crenata*," *Botanical Journal*, **2**: 111, 1913.

tion of the experimental garden is devoted to cultures of fasciated races, nothing further has been determined than that the fasciated character is inherited, that it is transmitted through non-fasciated individuals, that its apparentness depends upon nutrition, that it behaves as a

FIG. 17. TWO HERBARIUM SPECIMENS OF *x C. . . . arachnoidea.*

recessive character and that the fasciated character of the stem appears to be associated with split leaves and cup-shaped leaves. In a paper read before the Research Club of the University of Michigan on March 16, 1910, and announced under the title "The Identity and Inheritance of Teratological Characters," I showed that split leaves, ascidia, certain disturbances in the arrangement of the

flowers, supernumerary locules in the fruit, etc., may safely be taken as an indication of the presence of the fasciated character. More recently, Kajanus,[20] working

FIG. 18. SHOOT OF *x C. . . . arachnoidea*, WITH A LARGE NUMBER OF INFERTILE AND FEW FERTILE CAPSULES.

with different material, has fully confirmed the views which I expressed at the time. This is of particular in-

[20] Kajanus, B., "Polyphyllie und Fasziation bei *Trifolium pratense* L.," *Zeitsch. f. ind. Abst. u. Vererb.*, **7**: 63, 1912; "Ueber einige vegetative Anomalien bei *Trifolium pratense* L., *ibid.*, **9**: 111, 1913.

terest in connection with *Capsella arachnoidea,* since many of the plants which do not show a fasciated stem do show split leaves (Fig. 20) and a most peculiar whorling of the flowers (Fig. 21).

FIG. 19. FASCIATED PLANT OF × *C. . . . arachnoidea.*

The spatulate condition of the leaves of the seedling shown in Fig. 2 is believed to have been due to fasciation.

Capsella Bursa-pastoris arachnoidea, then, bears all the earmarks of a fasciated race. All of the three zygotic combinations which yield the *arachnoidea* type are homozygotic for *N*. The recent work of East and Hayes, and of Emerson on *Zea Mays* has shown that the fasciated

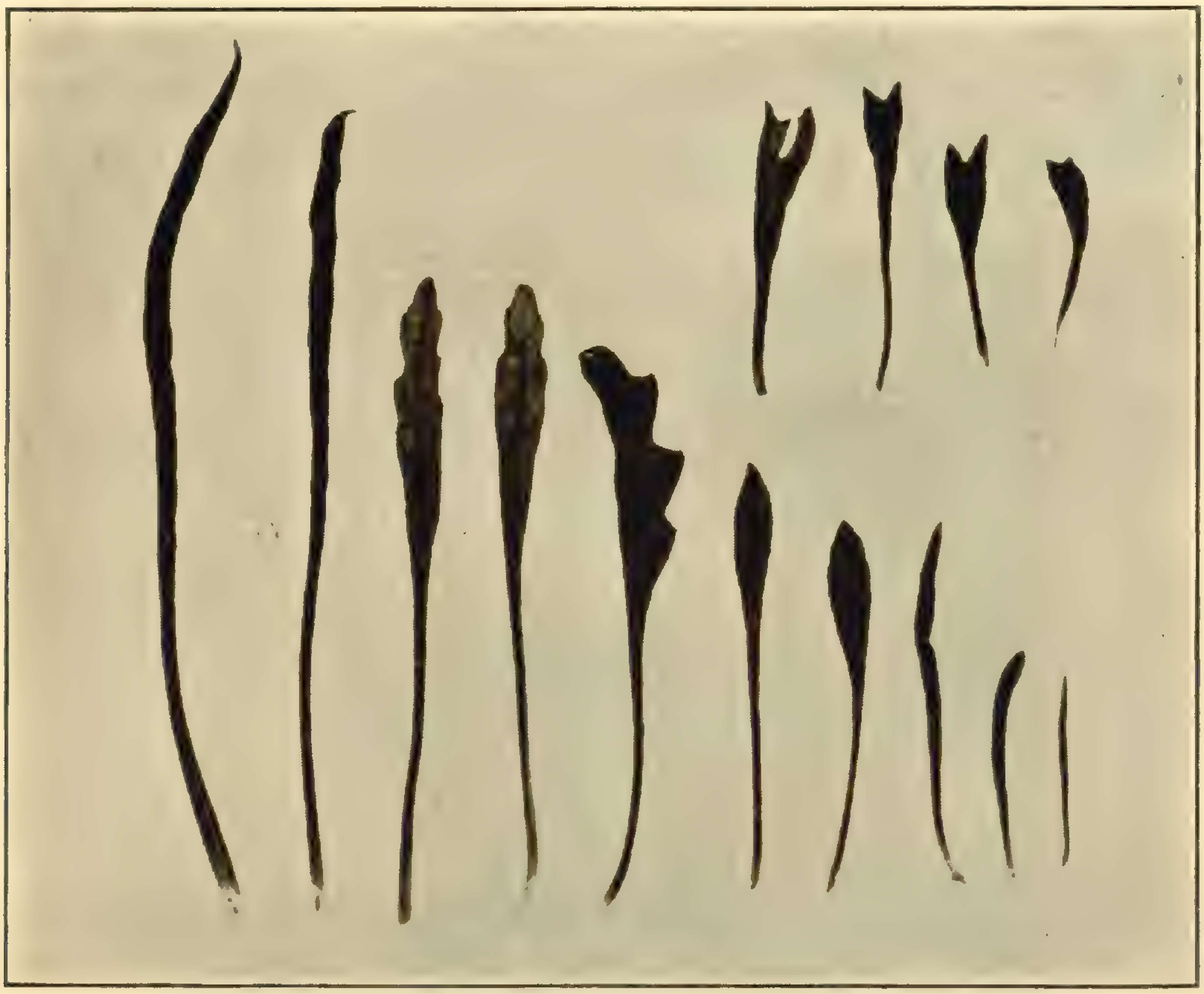

Fig. 20. Leaves of *x C. . . . . arachnoidea.*

Fig. 21. Abnormal Whorled Arrangement of the Flowers in Inflorescences of *x C. . . . arachnoidea.*

character is dominant, though Mendel, in his experiments with *Pisum umbellatum,* has shown it to be recessive. No fasciation, thus far at least, has been noted in the other forms used in these experiments.

Summary

A culture of *Capsella Bursa-pastoris* proved heterozygotic, yielding certain new forms (× *C. Bursa-pastoris Setchelliana,* × *C. Bursa-pastoris Treleaseana,* × *C. Bursa-pastoris arachnoidea* and × *C. Bursa-pastoris attenuata*), as well as certain forms already described by Shull (*C. Bursa-pastoris rhomboidea* and *C. Bursa-pastoris simplex*) in the proportion 4:2:4:2:3:1. The distinction between *simplex* and *rhomboidea,* both *inter se* and between them and the other forms, is readily made by any one familiar with Shull's investigations. These two plants agree in having the earlier leaves broad (Fig. 4). The climax leaves of *rhomboidea* and *simplex* show marked differences, especially as far as the incision of the blade is concerned. These incisions, in *simplex,* reach a depth equal to approximately one fourth of the width of the blade (Fig. 10). In *rhomboidea* the incisions are deeper, reaching the midrib in the homozygous form (Fig. 12). The leaves of the latter also show marked secondary lobes.

The distinction between × *C. Bursa-pastoris Setchelliana,* × C. *Bursa-pastoris Treleaseana* and × C. *Bursa-pastoris attenuata* is made with greater difficulty. They agree in having long and narrow first leaves. The climax leaves of *Treleaseana* and *Setchelliana* show marked incisions, exceeding one fourth of the width of the blade, and which may reach the midrib (Fig. 9). The latter form also may show marked secondary lobes.

Besides the phenotypes here mentioned occur two others, the one, × *C. Bursa-pastoris orbicularis,* with an almost orbicular first leaf (Fig. 13) and a climax leaf greatly resembling that of *simplex* (Figs. 14, 15), though differing in texture. This form has not been sufficiently studied, but is believed to be identical with one known to

occur in Europe. Finally there is × *C. Bursa-pastoris arachnoidea,* a sterile, linear-leaved form, with a weak stem and which frequently shows fasciation (Figs. 17–21). To facilitate a distinction between these forms, a key is appended:

a. Early leaves broad.	
b. Early leaves orbicular.	*orbicularis.*
bb. Early leaves twice as long as broad.	
c. Climax leaves incised to midrib.	*rhomboidea.*
cc. Early leaves not incised to midrib.	*simplex.*
aa. Early leaves long and narrow.	
b. Early leaves acicular.	*arachnoidea.*
bb. Early leaves 2½–3 times as long as broad.	
c. Climax leaves not incised to midrib.	*attenuata.*
cc. Climax leaves incised to or almost to the midrib.	
d. Secondary lobes pronounced.	*Treleaseana.*
dd. Secondary lobes absent.	*Setchelliana.*

It was found that, besides the genes *A*, *B*, *C* and *D*, whose existence was shown by Shull, there exists another gene, *N*, responsible for the narrow character of the earlier leaves. For the various forms, mentioned here, the following zygotic constitutions have been tentatively determined: *simplex, bbnn; rhomboidea, BBnn* and *Bbnn; Setchelliana, BbNn; Treleaseana, BBNn; attenuata, bbNn; arachnoidea, BBNN, BbNN and bbNN.* The zygotic constitution of *orbicularis* has not been determined.

As to the probable origin of × *C. Bursa-pastoris Setchelliana,* little can be said. It most probably results from a cross between *rhomboidea* and *attenuata* (*BBnn* × *bbNn*). This seems the most plausible explanation since, judging from herbarium specimens, both *attenuata* and *rhomboidea* occur throughout the United States. Unfortunately such an assumption necessitates an explanation of the origin of *attenuata.*

My thanks are due to the regents of the University of Michigan for the facilities placed at my disposal, to head-gardener Adolph Weiner for his constant care of the experimental plants, to Messrs. J. H. Ehlers, A. Povah, C. Oberlin and A. W. Murdock for assistance in classification of the seedlings and to the director of the Missouri Botanical Garden for the loan of herbarium material.

Conclusions

1. Besides the genes (*A, B, C, D*) discovered by Shull, there exists in *Capsella* a gene *N*, responsible for the narrow character of the early leaves of certain forms.

2. Absence of the gene *N* results in the formation of early leaves of a "broad" character.

3. The form designated *arachnoidea* is of hybrid origin, as are the forms *Setchelliana, Treleaseana* and *attenuata*.

4. × *Capsella Bursa-pastoris arachnoidea* is formed whenever the plant is homozygotic for *N*, whatever the constitution of the remainder of the zygote (*BBNN, BbNN, bbNN*), *i. e.*, a homozygous condition for the presence of a single factor may overshadow the influence of others.

5. Homozygocity for a single factor may be responsible for total, or almost total, sterility.

6. A knowledge of the early stages, as well as of the climax leaves, is essential for the classification of the phenotypes of *Capsella Bursa-pastoris*.

BIOLOGY OF THE THYSANOPTERA. II

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II. SEX AND THE LIFE CYCLE

Introduction

From observations made on the abundance of males in several species, Jordan (1888) was led to believe that there might be among Thysanoptera, as in aphids, an alternating life cycle; that is, that there might be a series of parthenogenetic generations during the summer, followed by a generation of males and sexual females in the latter part of the summer or in the fall. Coupled with this he suspected that there were winged forms in the parthenogenetic part of the cycle, and at least occasional wingless individuals in the sexual phase.

Uzel (1895), however, was unable to detect any indications of such a cycle. He held that there could be no question of parthenogenesis in a species in which males were abundant all the time or at intervals. Only in species in which the males were too rare to impregnate all the females would he admit parthenogenesis. To prove, in such a species, an alternating cycle like that of the aphids, it must, in Uzel's opinion, be shown that the males are abundant only at certain seasons. As Uzel was acquainted with no European species in which males were plentiful at but one season, he rejected Jordan's suggestion regarding an alternating cycle, and his view seems to have been accepted by thysanopterists since that time.

To Uzel's argument it may be objected that the presence of males, and even the occurrence of copulation, is no proof that parthenogenesis is wanting. For among the aphids and rotifers, the parthenogenetic and sexual females exist side by side. Nor is parthenogenesis in these two groups facultative (optional), as Uzel appears to assume for Thysanoptera; a female is either only

sexual or only parthenogenetic. Moreover, in the rotifers, females incapable of fertilization copulate as frequently as do those requiring fertilization, as was first shown by the work of Maupas (1890) on the rotifer *Hydatina.*

Presence of males and occurrence of copulation are, therefore, no proof of sexual reproduction. But even if we accept, as Uzel does, this criterion of sexuality, Jordan's view that there may be an alternating cycle would receive some support if it could be shown that males are more abundant at one season of the year than at other times. Casual observations made by me several years ago seemed to indicate this seasonal variation in the abundance of males. As the data then available were meager, no conclusion was drawn, but I subsequently undertook to obtain such data on a larger scale, by making extensive collections at all seasons of the year to determine the sex ratio. The following pages give these data, along with other observations bearing on sex or the life cycle.

I desire to acknowledge the assistance of my wife, by whom much of the labor of determining species and counting the sexes was done.

The Sex Ratio in Various Species of Thysanoptera

In making collections for the purpose of determining the sex ratio, the food plants were examined very carefully, torn apart if necessary, and every individual captured. This precluded the possibility of obtaining an erroneous sex ratio because one sex was more easily disturbed than the other. A few individuals escaped, but they could not have affected the sex ratio very greatly, and it was known from their size that they were sometimes of the one sex, sometimes of the other.

The sex in the suborder Terebrantia is readily determined by the presence of an ovipositor in the female and the rounded end of the abdomen in the male. In the suborder Tubulifera, the sex in *Anthothrips verbasci* was determined by the presence of two short, heavy spines,

one on each side of the abdomen of the male, near the end. As the specimens, when placed on a microscope slide, nearly always lie either on the dorsal or ventral side, these spines are nearly always readily visible if present. I used this criterion (mentioned in the re-description of the species by Hinds, 1902) only after having taken eleven pairs of this species copulating in nature, and observing in every case that the male possessed these spines, and that in the female they were wanting. In other Tubulifera, *e. g.*, *Anthothrips niger,* sex was determined by the longitudinal chitinous rod in the next to the last abdominal segment of the female. When the specimens were too opaque to observe this rod, they were cleared by boiling in caustic potash.

The data from these collections are given in the accompanying table. Unfortunately the collections could not all be made in one year, nor in the same locality. Those made from July 1 to September 18, 1912, were made at the University of Michigan Biological Station, Douglas Lake, Michigan; all others were made at Ann Arbor, Michigan. It is not probable that the results are greatly modified by collecting in two regions within the state. In this table the larvæ of all species are combined, as I am unable to distinguish with certainty the larvæ of several of the species here mentioned.

The important facts contained in this table are, it seems to me, the following:

Euthrips tritici appeared in spring at first only in the female sex. Males were first collected nearly a month later, and not until about the time fairly large larvæ were found elsewhere. Once the males appear, though their number fluctuates in the individual collections, they furnish a fairly constant proportion of the whole number (about one third).

The males of *Anthothrips verbasci* appear in the earliest collection of this species, and in considerable numbers throughout the season. The total proportion of males is 23 per cent., and the only considerable increases over

this percentage in individual collections are in the three collections made in August, and on October 7. Considering the large majority of females taken September 12, the abundance of males October 7 may be due in some way to

TABLE I

SHOWING NUMBER OF MALES AND FEMALES OF THE COMMONER SPECIES OF THYSANOPTERA CAPTURED AT INTERVALS DURING THE ACTIVE SEASON

Date	*Euthrips tritici*		*Anthothrips verbaski*		*Anthothrips niger*		*Thrips tabaci*		*Anaphothrips striatus*		*Thrips physopus*		*Chirothrips manicatus*		Larvæ, all Species
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	
Apr. 30, 1911	9	0													
May 5	7	0													
10	2	0													
17	17	0													
22	22	1					2	0			2	3			
24	30	2	174	30	20	0	6	0							7
June 1	41	17			18	0									6
7	40	62	52	10	42	0					4	7			3
15	21	27	47	8	18	0					1	2			25
21	87	11			4	0	25	0	1	0	0	1			1
29	11	6			4	0					2	7	1	0	5
July 3, 1912	14	25			1	0									46
4	21	7			7	0	1	0							72
5	3	0	82	29	2	0							2	0	1
11	0	3					1	0	95	18			187	1	16
16	7	2	43	25	7	0	16	0							3
17	6	1			31	0	42	0							
19	12	29					2	0	35	6			5	0	3
26			58	15											2
27	3	0							45	13					4
29	2	0					4	0			10	9			12
30													1	51	
31									42	15					1
Aug. 5	154	151							28	10	1	0			39
8	8	1	30	20					2	0	10	1			
9	16	13									1	0			
12													2	103	2
13			26	18											1
18	60	16					2	0			1	0			
20			18	17					39	48			2	36	21
21	40	3					10	0							13
Sept. 2	60	7					27	2	60	33					10
2, 1911	35	15			8	0	19	0			2	2			2
12			88	1											18
16	18	3					15	0					1	0	4
18, 1912									183	21					4
Oct. 7, 1911	32	13	23	27			19	0							12
14	18	4					11	0					2	0	
25, 1912	56	19					12	0			15	4			2
Nov. 9	27	3					12	0			1	0			
Total.........	879	441	641	200	162	0	226	0	530	174	50	36	203	191	

the dying of their food plants; but the greater proportion of males throughout August is probably significant. It should also be stated that I have collected adults of this species, of both sexes, from dead mullein spikes in late winter.

Anthothrips niger was found only in the female sex. There are no records of males of this species, so far as I am aware, in any published work.

Thrips tabaci was taken almost exclusively in the female sex, the two males found September 2 being the only ones I have ever collected.

In *Anaphothrips striatus* the total number of males is less than 25 per cent. On August 20 and September 2 the proportion of males is considerably greater than 25 per cent., especially on the former date, while at other times the proportion was nearly always less. The collection on August 20 can hardly have been erroneous by chance, for the figures given for that date are combined figures for two collections from different localities. In one of these collections there were 13 females and 14 males, in the other 26 females and 34 males. This strengthens the probability that the excess of males is significant.

Thrips physopus was collected in small numbers, but shows a fairly constant proportion of males.

Chirothrips manicatus presents curious phenomena. All the collections up to the end of July were made on timothy heads in a small patch a few feet square near the laboratory. On July 11 careful search revealed numerous females, but only one male. By July 19 almost all the thrips of this species were gone; only 5 specimens were obtained, and these were females. Less than two weeks later, however (July 30), on other timothy heads in the same small patch, there were found 51 males and but 1 female. No living thrips were taken here later, as the timothy died; but subsequent collections elsewhere, from timothy and bluegrass, show again almost exclusively males.

Additional Data Bearing on the Life Cycle and Sex

In view of the fact, to be discussed later, that *Anaphothrips striatus* has hitherto been known almost exclusively in the female sex, and is known to reproduce parthenogenetically, and the fact that in the collections here recorded the males constitute nearly 25 per cent. of the total, the question arises, are these males functional? If not functional in this species, are the males functional in other species? A number of observations and experiments I have made bear on these questions.

A single pair of *Anaphothrips striatus* was found copulating in nature, which Uzel would have considered proof that parthenogenesis did not occur. The testes of the males are plainly visible without dissection. Suspecting that they might not be fleshy organs at all, but chitinized structures, perhaps vestiges of testes, I boiled a number of specimens in caustic potash. The testes disappeared, from which I judge they are not merely chitinous bodies. I can say nothing of their cellular nature, owing to the loss of material killed and fixed for that purpose. Numerous sections of another species *Anthothrips verbasci*, however, reveal well-developed testes. Cell divisions (probably the spermatocyte divisions) and nearly mature spermatozoa in bundles were observed in these sections. Though the number of chromosomes could not be determined, it is an interesting fact that spindles in side view usually showed a lagging chromosome.

Finally, with further regard to the functioning of males, I have attempted to breed several species parthenogenetically. The results in the case of *Euthrips tritici* were so far encouraging that two larvæ appeared on the plant on which virgin females had been previously placed. But in these cases I could not be certain that the food plant was uninfected. Experiments with *Anaphothrips striatus* and *Anthothrips verbasci* gave negative results, but in each case failure to obtain young by parthenogenesis may have been due to the conditions.

Some observations on the place of pupation may also

be here recorded. The rarity with which the pupæ of most species are discovered in collecting suggested that they might not pupate on the food plant of the larvæ. Some species of thrips, for example, the pear thrips (*Euthrips pyri*), are known to pupate in the ground (Moulton, 1912). Since many of the species included in Table I may be found on white clover, which was abundant at Douglas Lake, the place of pupation of these species was tested in the following manner. A mass of the flowers of white clover was collected. The flowers were gently squeezed for some time to drive out all the adults. They were then placed in a vessel under cover. After two days, when the flowers were thoroughly dried, they were again gently crushed to make sure that all adults were driven out. At intervals from one to two weeks afterward, 15 adult thrips appeared on the inside of the glass cover. These were of three species, *Euthrips tritici, Thrips tabaci* and *Anthothrips niger*.

I have also frequently observed the pupæ of *Anthothrips verbasci* in mullein spikes, those of *Sericothrips cingulatus* on white clover, the pupa of *Trichothrips tridentatus* under the bark of the white oak, where the larvæ and adults live, and that of an undescribed species on willow galls along with larvæ of the same species. I judge from these observations that the majority of thrips pupate on the plants on which the larvæ live, and that their rarity in collections is due merely to concealment and sluggish habits.

DISCUSSION OF THE RESULTS IN RELATION TO THE LIFE CYCLE

From the data in Table I and the observations given above it is evident that there is considerable diversity in different species with regard to the life cycle, and diversity within the same species at different times or in different regions. First, as regards the mode of passing the winter, it would seem that in *Euthrips tritici* only the females survive that season. The reason for so believing

is that males could not be found in the spring until the females had been active long enough to have produced one generation of offspring. Males occur late in autumn, but must perish before the end of winter. Likewise, neither eggs nor larvæ live over winter, or larvæ would appear earlier in spring. In *Thrips physopus,* on the other hand, males were found as early as the females; hence, in the absence of any collection earlier than May 22, and in ignorance of the time required for development, I should assume that both sexes survive the winter. Both sexes of *Anthothrips verbasci* have been seen on dead mulleins in winter.

In species, like *Euthrips tritici*, whose males do not survive the winter, if fertilization of the early spring females takes place at all, it must occur in the fall. I do not regard my breeding experiments as proof of parthenogenesis in this species, but it is by no means improbable that parthenogenesis occurs. More rigorous experiments are needed.

As regards the mode of reproduction during the rest of the year, there is nothing in the sex ratio, as given in Table I, to suggest an alternating cycle in *Euthrips tritici.* In other species, it would be possible to interpret certain facts to mean that an alternation of parthenogenesis and sexual reproduction occurs, or did once occur. There is a well-marked increase in the proportion of males in *Anaphothrips striatus,* for example, in August. This is a particularly interesting species. Hinds (1902) saw only the female of this species, though he mounted and examined over a thousand specimens, and he bred it parthenogenetically in the laboratory for months. What purported to be the male was described by Cary (1902), from Maine, but the specimens described were evidently those of another species. The first males ever recorded were described by Shull (1909), two specimens among probably two hundred females. It is remarkable, therefore, that in the vicinity of Douglas Lake there should be nearly 25 per cent. of males. Whether

the presence of numerous males is dependent on climatic conditions, or whether it is a racial difference, there is at present no way of deciding. The weather was unusually cold during the summer in which these records were made, and it is desirable that the effect of temperature be experimentally determined. The presence of males in goodly numbers throughout the summer, the occurrence of copulation in nature, and the failure of an attempt to breed the species parthenogenetically, leave, as the only reason for suspecting that it may have been parthenogenetic at Douglas Lake, the fact that it is parthenogenetic elsewhere. But if the species is parthenogenetic in one region and sexual in another, it is not difficult to believe that it may be both parthenogenetic and sexual in the same region. It is difficult to decide whether the well-marked increase in the proportion of males in August and early September should be regarded as evidence of such an alternation, or as due to a period of cold weather or other climatic factor, or as a hereditary remnant of the sexual phase of an alternating cycle once possessed by the species. Only experiment, and perhaps cytological study, can decide this question.

A similar but less marked increase in the number of males is seen in *Anthothrips verbasci,* also in August. In that month the proportion of males rose from about 20 per cent. to 40, or even nearly 50 per cent. In this species the increase may be due to the late date at which the first brood of larvæ becomes mature. The life history of this species is longer than that of most of the suborder Terebrantia, and may appear to be still longer because enemies destroy many of the larger larvæ. For these reasons, in the region of Douglas Lake, the first generation of larvæ may not become mature until nearly August. If this assumption is correct, the proportion of males found prior to August is the proportion that survive the winter. This explanation receives support from the cytology of the germ cells. As stated above, there is a lagging chromosome in the spermatocyte divisions, which suggests

the probability that there are two classes of sperm associated with sex, as in the bugs and many other animals, and that therefore the sexes should be approximately equal in numbers. The 40 to 50 per cent. of males in August accord fairly well with this explanation.

This explanation would not, however, account for the increase in the number of males in late summer in a species whose life history is much shorter than that of *Anthothrips verbasci.* Thus, in *Anaphothrips striatus,* Hinds states that the entire life history is passed through in 12 to 30 days. Even in a cold season, such as that of 1912 at Douglas Lake, therefore, the life history can not have been so long that the first adults would emerge in the middle of August. The increase in the number of males of *Anaphothrips* in August and September is not to be explained, therefore, as due to the first appearance of a new brood at that time.

Thrips tabaci likewise affords interesting, even if meager, evidence regarding the seasonal occurrence of males. In this species males are exceedingly rare. Hinds (1902) redescribed the male in quotation marks, from which it is to be inferred that he did not have specimens. In my own collecting, though the females were quite common, I never saw a male until the summer of 1912. Then two specimens were taken September 2, as shown in Table I. These irregularly occurring males can hardly be functional, so that *Thrips tabaci* is still probably to be regarded as wholly parthenogenetic. But their appearance in late summer may be the vestige of a former sexual phase, and may be caused now, as the sexual phase probably was in part formerly caused, by climatic conditions.

Chirothrips manicatus presented, at Douglas Lake, an anomalous condition. As shown in Table I, and stated more explicitly above, females were abundant in a given small area early in July, but practically no males were present. Then, so far as I could determine by painstaking collections, the females disappeared; almost no adults of either sex, and not many larvæ, were to be found. Two

weeks later, however, males were found in the same area in large numbers. As these males were wingless, they had probably not immigrated. The only other explanation that occurs to me is that the larvæ were present in considerable numbers at the time of the earlier collections, but in the flowers, not among the spikelets of the timothy, so that I did not discover them; and that the female larvæ reached maturity much earlier than the males. In any case, it is difficult to see how the males can have been functional, when the two sexes occurred at different times. If such conditions recur frequently, *Chirothrips manicatus,* even though it produces many males, must be parthenogenetic.

SUMMARY

The principal conclusions reached in the second part of this work may be stated as follows:

Some species of Thysanoptera pass through the winter in both sexes, in others the males perish. In none of those studied does the egg or larva live over winter.

Pupation of most of the species of Thysanoptera studied occurs on the food plants where the larvæ live, notwithstanding that the pupæ seldom appear in collections.

From the determination of the sex ratio, *Euthrips tritici* shows no indication of an alternating life cycle. It is probably sexual throughout the active season, though this is not proven.

Chirothrips manicatus occurred abundantly in both sexes, but the two sexes appeared at different seasons. The explanation of this phenomenon is doubtful.

An increase in the number of males in *Anthothrips verbasci* in late summer may be explained as due to the great length of the life history and to selective mortality during the winter, without assuming an alternating life cycle.

Anaphothrips striatus, a species which has hitherto been known almost wholly in the female sex, produced about 25 per cent. of males at Douglas Lake. This may

be due either to climatic conditions or to racial differences. Sexual reproduction was not wholly proven, but seems probable. An increase in the number of males in late summer in this species and in *Thrips tabaci* might be interpreted as indicating a sexual phase, or the vestiges of a sexual phase that existed in the species formerly. Jordan's belief in an alternating life cycle, which was rejected by Uzel, thus receives some measure of justification.

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SHORTER ARTICLES AND DISCUSSION

BARRIERS TO DISTRIBUTION AS REGARDS BIRDS AND MAMMALS

THE geographical range of any species of animal may be likened to a reservoir of water in a mountain canyon. The confining walls are of varying nature. A concrete dam, absolutely impervious, may retain the water at one end. Along either side the basin's walls differ in consistency from place to place. The substratum varies in porosity, at some points being impervious like the dam, at others permitting of seepage of water to a greater or less distance from the main volume. The water continually presses against its basin walls, as if seeking to enlarge its area. And it may succeed in escaping, by slow seepage through such portions of its barrier as are pervious or soluble, or by free flow through a gap in the walls, if such offers. The area occupied by the water will extend itself most rapidly along the lines of least resistance.

Every species has a center or centers of abundance in which favoring conditions usually give rise to a rate of reproduction more than sufficient to keep the critical area stocked. A tendency to occupy a larger space results, because of competition within the species: individuals and descent-lines multiply and travel radially, extending those portions of the frontier where least resistance is offered. Such radial dispersal takes place slowly in some directions, more rapidly in others, according to the degree of passability of the opposing barriers. These barriers consist of any sort of conditions less favorable to the existence of the species than those in the center of abundance.

Theoretically, sooner or later and in all directions, every species is absolutely stopped. But as a matter of undoubted fact most barriers are continually shifting, and the adaptability of the animals themselves may be also undergoing continual modification; so that perfect adjustment is beyond the limits of possibility so long as topography and climate keep changing. The ranges of species may thus be constantly shifting. Descent-lines may move about repeatedly over the same general region, like sparks in the soot on the back of a brick fireplace.

Yet, in all of our studies, of but a few years' duration, the

time element is reduced almost to a negligible quantity, and we may look upon the areas occupied by each species as, for the time of our observation, fixed. We are thus enabled to compare one with another, and because of the large number of the species, we can infer a good deal as to the nature of barriers in general, at least as regards birds and mammals. It is even conceivable that; with sufficient refinement in methods, the inquirer might in time find himself able, from a comparative study of the ranges of rodents, for example, to establish the identity of all of the external factors which have to do with the persistence of each of the species; in other words to analyze the "environmental complex" into its uttermost elements—as regards the existing species of rodents in their recent development.

The most obvious kind of barrier to distribution is that consisting of any sort of physical, or mechanical, obstruction. Such obstruction affects directly the *individuals* of a species encountering it, either by stopping their advance or by destroying outright such as attempt to cross it. As barriers of this nature, are to be cited land in the case of purely aquatic mammals, and bodies of water to purely terrestrial, especially xerophilous, mammals. In each case the width of the barrier has to do with the degree of impassability. Oceans and continents are most perfect, and affect a large proportion of the species. The comparatively narrow Colorado River is a barrier of the first rank, but only to a certain few desert rodents. Mechanical barriers, where they exist at all, are clearly recognizable.

It is to be observed, however, upon considering the birds and mammals of a whole continent, that by far the greater number of species are delimited in range without any reference to actual land and water boundaries; more explicitly, their ranges fall far short of coast lines. The barriers here concerned are intangible, but nevertheless powerful. By their action the spread of species, genera and families is held in check as surely as by any tangible obstruction.

By these invisible barriers the *individual* may not necessarily be stopped at all, as with animals of free locomotion; but the *species* is affected. For example, the mocking bird in its Californian distribution is closely confined to those parts of the state possessing certain definite climatic features; but vagrant individuals, especially in autumn, occur far beyond the limits of these restrictive conditions. Carnivorous mammals are well

known to be subject to sporadic wanderings on the part of individuals, but the *species* is kept in set bounds by some potent but invisible set of factors. The very fact that *individuals* are quite capable of temporarily transgressing these bounds and yet do not overstep them *en masse* emphasizes all the more the remarkable potency of this category of barriers as regards species and higher groups.

Our geographic studies lead us to designate among these relatively intangible barriers: (1) increase or decrease in prevailing temperature beyond certain critical limits, according to the species concerned; (2) increase or decrease in prevailing atmospheric humidity beyond certain limits; (3) modification in food-supply and appropriate breeding and foraging ground. The limits set by each of these factors will vary with the physiological peculiarities of the organism considered; in other words the inherent structural equipment of each animal figures importantly. In these three sorts of barriers will be recognized what have been called "*zonal*," "*faunal*" and "*associational*" delimitation, each of which I will now try to define.

Two schools of faunistic students are represented among American zoo-geographic writers of the present day. One, of which C. H. Merriam is the most prominent exponent, sees in temperature the chief cause controlling distribution, and deals with the ranges of species in terms of "life zones." The other school, of which C. C. Adams, A. G. Ruthven and Spencer Trotter are active advocates, assigns to temperature but a minor rôle, looking rather to a composite control, of many factors, resulting in ecologic "associations," of which plants are essential elements, and which are to be further explained on historical grounds. The two sets of areas thus defined do not by any means correspond. Yet the reviewer can not fail to note, here and there, places where boundaries coincide, and such coincidences are so frequent as to be suggestive of real concordance in some significant manner. Is it not probable that both schools are approximately correct, the difference in mode of treatment being due to different weights given the different kinds of evidence, or, in other words, to difference in perspective?

Every animal is believed to be limited in distribution zonally by greater or less degree of temperature, more particularly by that of the reproductive season. When a number of animals (always in company with many plants similarly restricted)

approximately agree in such limitation they are said to occupy the same life zone.

The observation of this category of distributional delimitation is particularly easy in an area of great altitudinal diversity like that comprised in the southwestern United States. The writer is led to wonder if those authors who minimize the importance of temperature have ever been privileged to travel extensively, and *carry on field studies,* outside of the relatively uniform eastern half of North America!

Study of any area which varies widely in altitude and hence provides readily appreciable differences in daily temperature from place to place brings conviction of the very great effectiveness of temperature in delimiting the ranges of nearly all species of animals as well as of plants. Particular attention may be called to the pertinent results of Merriam's survey of Mount Shasta.

But temperature is not to be considered the only delimiting factor of environment, though its possible overemphasis by the Merriam school seems to have led some other persons to believe that this view is held. In fact it becomes evident, after a consideration of appropriate data, that very many species are kept within geographic bounds in certain directions only by an increasing or decreasing degree of atmospheric *humidity.* By plotting the ranges of many animals as well as of plants coincidence in this regard is found in so many cases as to warrant the recognition of a number of "faunal areas"—on the causative basis of relative uniformity in humidity. It is probable that every species is affected by both orders of geographic control.

The reader may enquire as to the grounds for employing the widely used terms zone and fauna in the restricted sense here prescribed. In reply, it may be said that this is not an innovation, but is an adoption of a usage which has come about historically among a certain group of workers in the geography of vertebrate animals in North America. The writer recognizes the fault in imposing restricted meanings upon old terms, but he also hesitates at coining new words.

As to which is *the more* important, assembled data seem to show that more genera and higher groups are delimited by zonal boundaries than by faunal boundaries. The arresting power of temperature barriers would therefore seem to be relatively the greater.

In the third category of distributional control there is a conspicuous association of the majority of so-called adaptive structures of animals (often of high taxonomic value) with certain mechanical, or physical, features of their environment. An animal may thus intimately depend upon certain inorganic or organic peculiarities, or both, of a given area, and be unable to maintain existence beyond the limits of occurrence of those features of the environment. Tracts of relatively uniform environmental conditions, including their inanimate as well as living elements, are here called *associations*.

After a consideration of all the birds and mammals occurring both within the state of California and elsewhere as far as the writer's knowledge goes, associational restriction appears to be governed by the following three factors, of relative importance in the order named.

1. Kind of food-supply afforded, with regard to the inherent structural powers of each of the animals concerned to make it available.

2. Presence of safe breeding places, adapted to the varying needs of the animals, in other words depending upon the respective inherent powers of construction, defence and concealment in each species concerned.

3. Presence of places of temporary refuge for individuals, during daytime or nighttime, or, while foraging, when hard-pressed by predatory enemies, again correlated with the respective inherent powers of defence and concealment of each species involved.

It is believed that the geographical distribution of any animal is correctly diagnosed in terms of each of the three main groupings here suggested. In other words an animal belongs simultaneously to one or more zones, to one or more faunas, and to one or more associations. No one of these groupings can be stated in terms of the other, any more than a person can compute liquids by candle-power, or weight in miles. The constituent species within each of these groupings always belong to the other two. To illustrate: the southern white-headed woodpecker inhabits the coniferous forest association of the San Bernardino fauna of the Transition zone; the Abert towhee belongs to the mesquite and the quail-brush associations of the Colorado Desert fauna, of the Lower Sonoran zone; the Pacific shrew belongs to the upland riparian association of the northern coast redwood fauna of the Transition and Boreal zones.

Classification of Barriers to Species as Regards Birds and Mammals

Barriers:

A. Intangible.

- (*a′*) Zonal (by temperature).
- (*b′*) Faunal (by atmospheric humidity).
- (*c′*) Associational.
  - (1) By food supply.
  - (2) By breeding places.
  - (3) By temporary refuges.
    - (Each of these three with regard to the inherent structural characters of each species concerned.)

B. Tangible (mechanical).

- (*a″*) Land to aquatic species.
- (*b″*) Bodies or streams of water to terrestrial species.

The above categories are believed to include all the factors commonly involved in checking the spread of species of birds and mammals. It is possible that inter-specific competition may sometimes occur where associational homologues meet. But even here it becomes a matter of relative associational fitness which determines supremacy and consequent ultimate limits of invasion of the forms concerned.

A mountain range, mechanically speaking, is no barrier at all, *per se*, as frequently alleged. Only as it involves zonal or faunal barriers does it affect distribution. The same is true of a valley or a desert.

As far as contemplation of cases has gone, the writer's experience has led him to believe that the outlines of the ranges of all birds and mammals may be accounted for by one or more of the factors indicated in the analysis here presented. And as detailed knowledge of the facts of geographical distribution accumulates, the delimiting factors become more and more readily detectable. By such a study, of *comparative distribution,* it seems possible that the ranges of birds and mammals may become subject to satisfactory explanation.

When considered in its historical bearing, the problem of barriers concerns itself intimately with the origin of species. It is believed by the writer that only through the agency of barriers is the *multiplication of species,* in birds and mammals, brought about.

The present contribution is abbreviated from a general discussion of certain distributional problems which forms part of a paper to appear from the University of California press and which treats in detail of the birds and mammals of the lower Colorado Valley, in California and Arizona.

JOSEPH GRINNELL

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YELLOW VARIETIES OF RATS

IN a recent number of the NATURALIST I described a yellow variety of the common rat (*Mus norvegicus*) which in recent years made its appearance in England and is now a recognized variety among fanciers. Dr. John C. Phillips and Professor L. J. Cole have both called my attention to a fact which I had overlooked; namely, the occurrence of a yellow variety in another species of rat (*Mus rattus*). Bonhote described the occurrence of this variety in Egypt in 1910 and has since found by experiment (1912) that the yellow variation of *Mus rattus* is recessive in heredity precisely as it is in *Mus norvegicus.* The fact that the yellow variation in mice is dominant in heredity, but can not be obtained in a homozygous condition, stands, therefore, as a phenomenon all the more singular and striking.

W. E. CASTLE.

BUSSEY INSTITUTION,
March 3, 1914.

NOTES AND LITERATURE

HEREDITY AND "THE INFLUENCE OF MONARCHS"

In "The Influence of Monarchs" (xiii and 422 pp., 1913, The Macmillan Co., New York, $2.00) Dr. Frederick Adams Woods makes a second and firmer step along the path entered on with his interesting "Mental and Moral Heredity in Royalty" published in 1906. Dr. Woods's goal in beginning and continuing his analysis of the character of royalties and the circumstances of their reigns is one probably not immediately to be reached but also probably one not impossible of attainment. It is indeed not one goal that he has before him, but two, the ways to which lie close together and parallel. One is the establishing of a new science of history to be called historiometry; the other is the making apparent of the dominance of heredity over environment in determining human fate.

That the methods and even the aims of most historical study are not satisfying to all historical students is made obvious by the constant complaining of historians to and of each other. There are two conspicuous groups of these protestants, one demanding more interest, more imagination, a more literary treatment of historical fact, and the other demanding a more significant, more inductive, more scientific treatment. The former wants more "humanity," the latter more biology, in history. Dr. Woods is of the latter group.

But Dr. Woods is not primarily of any historical camp. He is biologist, especially evolutionist and student of heredity. However, he marches very boldly into the ranks of the students of historical human history—to distinguish thus the last few thousand years of human history from the earlier many thousand years of it—with the new methods and results of his historiometry, just as Pearson, several years ago, invaded the biological camp with his biometry. Something of historiometry in history there has always been, just as there has always been something of biometry in biology. But these reformers want to make history and biology wholly, or, at least, most importantly, sciences of measure. And each of them finds that his use of measure in them leads him to discover that the facts that he is measuring offer, in the new significance they are thus made to yield, a special argument for some particular one of the major factors in evolution.

Biometry emphasizes the enormous importance and significance of variation in all living things; historiometry reveals the enormous importance of heredity in human life and the affairs of society.

After an introductory chapter stating the need of a new interpretation of history and of new methods of getting at this interpretation, and a following general chapter further elaborating and expanding his views concerning "the philosophy of history and historiometry," Dr. Woods plunges into a series of compact histories of France, Castile, Aragon, United Spain, Portugal, The Netherlands, Denmark, Sweden, Russia, Prussia, Austria, Turkey, Scotland and England. In each of these he presents a swift summary of the economic and political conditions (success in wars, increase in territory and prestige, prosperity, advance, failures in war, loss of prestige, poverty, retrogression) of these nations in the various reigns of a period of about 500 years for each country, together with a statement of the personal traits of each monarch. In all, three hundred and sixty-eight monarchs, regents or other rulers, royal or non-royal, and correspondingly, three hundred and sixty-eight sets, or periods, of national conditions, are presented.

From these data is derived the very positive and important conclusion that the dominant causal influence in determining the character of national, political and economic conditions has been the personality of the monarchs, and that the prime determinant of this personality is heredity and not environment.

A host of possible criticisms and objections to the method, its results and their interpretation, leaps into every one's mind. Well, they are all—or all that I have so far been able to formulate—anticipated, and ingeniously, and usually convincingly, answered. At least they are anticipated and discussed. In this the book reminds one of Darwin's "Origin of Species."

To all who have read "Heredity in Royalty" this new book of Dr. Woods will need no recommendation of its interest and importance. To those who have not, and are interested either as historian, biologist, or natural philosopher in human history and the bionomic factors that control it, "The Influence of Monarchs" may be strongly recommended as an original and very suggestive treatment of the subject. To students of heredity the book is a necessary library addition.

V. L. K.

Stanford University,
California

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ECTOPARASITES OF MAMMALS

PROFESSOR VERNON LYMAN KELLOGG

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I

THE wingless permanent ectoparasites of mammals are chiefly of two groups, namely, the Mallophaga, or biting lice, which feed on the hair and dermal scales, and the Anoplura, or sucking lice, which feed on the blood. Certain mites and ticks, a few of the Pupipara (degenerate flies) and almost all of the fleas are also ectoparasites of the mammals, but the fleas, numerous and economically important as they may be, are not permanent parasites, for they live as larvæ not on the host of the adult, but in cracks and crevices in floors, or in the soil and elsewhere that the organic detritus used by them as food may be found. The adults, too, hop on and off their host, and often change from one host individual to another, and even from one host species to another. So that the problems of distribution and species-forming with which I am particularly concerned in my studies of the ectoparasites are not at all the same in such impermanent form as the fleas as in those truly permanent forms, the Mallophaga and Anoplura.

In these latter there occurs an extraordinary limitation of the parasite individuals and their immediate progeny and future generations to specific and even individual hosts (and *their* progeny and future generations), so that the Mallophagan and Anopluran fauna of any mammal usually represents a closely inbred family strain biologically iso-

lated from the rest of the individuals comprising the particular species represented by it. This brings about certain striking conditions of abundant small variation and subspecific (or intraspecific) distinction, which, however, because of the general similarity of habitat, food and habit, do not tend to grow rapidly into large (specific, generic, family) differences. The hundred or more species of Mallophaga so far recorded from mammals have, until very recently, all been ascribed to two genera, of which one included nearly nine tenths of the total number of kinds. There has been made a beginning—and not a particularly convincing one—at breaking up this inclusive genus (Trichodectes). It is a movement suggested more by the needs of convenience than the needs of expressing a biological situation. Similarly, although not representing so extreme a condition of likeness, the Anoplura, also including about a hundred parasite species (occurring only on mammals) have been, until recently, divided into but half a dozen genera, with the great majority of the species included in one. Certain aberrant forms found on man, the monkeys, the elephant, and on seals and walruses have always made necessary the recognition of four or five quite distinct genera. Attempts, however, are now being made to break up the unwieldly genus *Hæmatopinus.*

As this paper is, in effect, a continuation of my paper on "Distribution and Species-forming of Ecto-parasites" published in THE AMERICAN NATURALIST in March, 1913, which devoted itself to a consideration of the Mallophaga (some 1,400 species as so far known) found on birds, and to the problems presented by their conditions of life and their host and geographic distribution, I can dispense with any further account of the special biology of these parasites by referring the interested reader to this former paper. In it I have set out rather fully the special structural and habit features of the Mallophaga. Except that the Anoplura take blood, rather than feathers and hair, for food, and have specially modified

mouth parts to do it with, and are perhaps even more specialized in their physiological adaptations to their host than the biting lice, most of the general remarks made concerning the Mallophaga will apply to the sucking lice also.

In their peculiar special relations to their hosts as permanent ectoparasites on them, wingless, and reluctant to migrate even with opportunity, and so fitted physiologically to their parasitic life that they can not live for more than a few hours (or, at most, and exceptionally, days) off the bodies of their hosts, the Anoplura and Mallophaga are alike. And hence the conditions and problems of their distribution and species-forming are practically the same for the two groups.

The thesis that I have maintained, on a basis of the conditions presented by the bird-infesting Mallophaga, I now wish to test by the conditions presented by the mammal-infesting Mallophaga and Anoplura. This thesis is, in fewest words, that the host distribution of these wingless permanent ectoparasites is governed more by the genetic relationships of the hosts than by their geographic range, or by any other ecologic conditions. The fact, proved by abundant cases, that two host species of wholly distinct geographic range and with no possible opportunity for contact such as would permit of the migration of wingless parasites from one to the other, may have, nevertheless, one or more parasitic species common to them both, is associated almost always with the further fact that these common hosts are closely related genetically. They are most often of the same genus or of closely allied genera; they are almost certainly always of the same subfamily or family. The explanation for the possibility and the reality of this interesting host distribution I find in the hypothesis that the common parasite species has persisted unchanged from a common ancestor of the now divergent but allied host kinds.

Also, if it be true that genetic relationship is the deter-

mining factor in accounting for the host distribution of the parasites, then it is also true that the distribution of the parasites will indicate in some measure the genetic relationships of the hosts, and that occasional aid in determining the genetic affinities of birds and mammals of doubtful relationships may be had from a study of their parasitic fauna. In my paper already referred to I have pointed out some suggestive cases of this sort in connection with the birds and their parasites.

In examining the conditions existing among the mammals and their Mallophagan and Anopluran fauna, the first necessity was the compilation of a complete record or catalogue of mammalian hosts and their parasites, together with the record of the actual locality of each finding of parasites, together with a general record of the geographic range of all the various hosts. This catalogue, or set of records, I have now completed, and despite its meagerness compared with the similar catalogue of the bird hosts and their Mallophagan parasites from which the notes for the former paper were drawn, it contains enough records of interest to make worth while a preliminary report on the condition obtaining among the mammals and their parasites.

It is unfortunate that, although there are nearly one fourth as many mammal species as bird kinds, only about one hundred mammals figure in the Mallophagan host list, while Mallophagan parasites have been taken from over eleven hundred bird species. Also, only one hundred different Mallophaga have been taken from mammals, while about fourteen hundred have been taken from birds. Of the Anoplura, which are found only on mammals, records have been made from about one hundred host species, these records referring to just about the same number of Anopluran kinds. Thus the mammalian host catalogue with its list of parasites is a short one; as far as it goes, however, it is thoroughly interesting and suggestive.

In working up the records I have used Trouessart's

"Catalogus Mammalium" as an authority for the synonomy of the hosts, and my own judgment, based on a considerable personal knowledge of the parasites and on a careful consideration of all the more intelligible literature of the two groups, as a last court for the synonomy of the Mallophaga and Anoplura species. The synonomy of the parasites I have, however, not pushed far.

With so much of introduction and explanation we may come to a swift résumé of the results of a scrutiny of these records, proceeding by sequence of the mammalian orders, and referring to either or both groups of parasites as they may happen to be represented in the parasite records of the successive host groups.

II

The Marsupialia are represented in the host list by half a dozen species of kangaroos and wallabies (family Macropidæ) all from Australia, and a wombat, *Phascolomys ursinus* (family Phalangeridæ), from Tasmania (also S. Australia?). From all of these hosts only Mallophaga are recorded, no Anoplura having yet been taken from a marsupial. The six species of kangaroos represent three genera (Macropus, Petrogale and Æprymnus), and their Mallophaga are of seven species, representing four genera. Four of the species belong to the genus Boopia, and I strongly suspect are not all different. In addition there is one Trichodectes, from *Petrogale penicillata,* one Latumcephalum, from "wallabies," and one Heterodoxus, which is recorded from *Macropus giganteus* in Australia as well as from the same host in the Jardin des Plantes, Paris. It is also recorded from an undetermined wallaby in Victoria and one in Queensland, as well as appearing in three other records from "kangaroo" or "wallaby" from Australia. The parasite of the wombat is a species of Boopia, and it has been twice recorded from the same host. It is interesting that the kangaroo in the Jardin des Plantes harbored, even after some period of captivity, only its own proper para-

sites without accepting new ones from its many, various and closely pressing neighbors.

Of the four Mallophagan genera found on the kangaroo, three, namely, Boopia, Latumcephalum and Heterodoxus[1] are peculiar to them. The third genus, Trichodectes, is represented by but a single species which has been recorded but once. This is the common Mallophagan genus of mammals generally. The record is perhaps a good one, but its lack of confirmation by being unrepeated either for the same species or for any other species of Trichodectes, is suggestive. Heterodoxus, Latumcephalum and Boopia are two-clawed genera; that is, they are Mallophagan forms which belong to a family all the other genera of which are confined to birds. The characteristic structural difference between the mammal-infesting Mallophaga and the bird-infesting species is the presence in the first group of a single claw on each tarsus, and in the second of two claws. This difference is plainly an adaptive one concerned with the fitting of the foot for the seizing of hairs and scrambling about among them, on the one hand, and the manipulation of feathers and moving about on them, on the other. In examining living specimens under the microscope the special use and fitness of the feet, in the one case adapted to hairs and in the other to feathers, is obvious. However, Heterodoxus, Latumcephalum and Boopia, and, in addition, perhaps one other doubtful genus, represented by one species, and perhaps two or three species of another two-clawed genus, constitute exceptions to the general rule. It is of decided interest to note that the only genera of two-clawed Mallophaga found exclusively on mammals are limited to the Marsupials. The antiquity and isolation of

[1] The single valid species of this genus—the two or three that have been named are undoubtedly all the same—has also been recorded from dogs! In fact specimens in my own collection were received with the record "from Japanese dog." And Enderlein has recorded it from a dog from China and Neumann from a dog from Formosa. Yet dogs ordinarily do not harbor this parasite, and kangaroos and wallabies do. It seems necessary to believe that the dog host records indicate cases of straggling from kangaroos in zoological gardens or menageries.

this host group strongly suggests that the one-clawed condition common to all other mammal-infesting Mallophaga is a derivative from the original two-clawed condition characteristic of the parasites of birds and of these ancient mammals. The two-clawed condition is, of course, the one common to insects generally and is characteristic of the Atropids, in whom I am inclined to see the ancestors, or near-ancestors, of the Mallophaga. All of the Anoplura, it may be added, which are exclusively mammal-infesting, are one-clawed.

In this connection the suggestiveness of the fact that in face of the examination of many specimens of half a dozen species of kangaroos and wallabies, no Anoplura have yet been found on the Marsupials, may be referred to. I am coming strongly to believe that there is no such wide ordinal separation of the Mallophaga and Anoplura as our clinging to the fetich of "biting and sucking mouth-parts" as basis for radical classificatory separation has led us to effect. I believe, with Mjöberg, that the two groups of parasites have a fairly near genealogical affinity, their differences, which are particularly those of mouth-parts, being adaptive rather than palingenetic in character. The Anoplura have gone on from the Psocid-Mallophagan condition to a more specialized parasitic habit, and are the extremes of a general line of ecto-parasitic evolution. The absence of sucking lice from the kangaroos may mean that the Marsupials are older than the Anoplura! No other considerable group of mammals, except certain families of strong-smelling Carnivora, is free from the blood-sucking parasites.

There are but two Edentates in the host list, one, the Cape Ant bear, *Orycteropus afer* (family Orycteropodidæ) of south and central Africa, harboring a sucking louse, of genus and species peculiar to it, and the other, the three-toed sloth, *Bradypus tridactylus* (family Bradypodidæ) of eastern South America, harboring a Mallophagan of species peculiar to it but of the genus *Gyropus* which is the less scattered, although still rather catholic,

genus of the two large ones characteristic of the mammals.

The large order Ungulata, with its numerous domesticated and semi-domesticated species, is a favorite host group with both Mallophaga and Anoplura. Altogether[2] about thirty Anoplura and two dozen Mallophagan species are recorded from fifty host species representing nine Ungulate families.

The family Elephantidæ is represented by the African and Indian elephants, recognized as distinct species of distinct geographic range. They both harbor a common Anopluran species, *Hæmatomyzus elephantis,* of species, genus and family peculiar to the elephants. Fahrenholz has given the varietal name *sumatranus* to specimens of these sucking lice taken from an Indian elephant in Sumatra. Records show that the parasites have been taken from their elephant hosts not only in Africa and Asia, but in various zoological gardens, as Paris, Hamburg and Rotterdam.

The small family of Hyracidæ, or conies, is represented in the host list by two species and perhaps a third one, one of which, the Syrian coney of west and south Asia, harbors one Anopluran and one Mallophagan, while from the other, the Cape coney of South Africa, the same Anopluran species is recorded as well as another of the same genus. This record of a second species is from a coney in the London Zoological Gardens. From the possible third species of Hyrax (taken in the African Congo and perhaps, but not probably, also a Cape coney), a second Mallophagan species is recorded of the same genus, Trichodectes, to which that of the Syrian coney belongs.

In the family Equidæ three species, the horse, the donkey and Burchell's zebra, all suffer from the infestation of a common Anopluran species, *Hæmatopinus asini.* In addition, the horse and the zebra have a common

[2] The synonomy in the parasite records, and indeed in the host records as well, is a vicious tangle. I have done the best I can, for the present.

Mallophagan parasite, *Trichodectes parumpilosus,* while the horse and donkey have another common biting louse, *Trichodectes pilosus.* Two varieties of *Trichodectes parumpilosus* have been named by Piaget, one from the zebra and another from "little horses of Java."

The pigs (family Suidæ), of which three wild African species besides the familiar animal of the barnyard are found in the host list, are infested by two (perhaps three) species of Anoplura and one (a not too certain record) Mallophagan. *Hæmatopinus suis* is found on the domestic *Sus* all over the world, while *Hæmatopinus latus* of Neumann, *H. phocochoeri* of Enderlein and *H. peristictus* of Kellogg and Paine, which are almost certainly all one species, are recorded from the wart hog, *Phacochœrus æthiopicus* from Nyasa-land, Africa, and probably also from another wart hog species from Africa, and the Red River hog, *Potamochœrus chœropotamus* from Nyasa-land, Africa. In addition *Potamochœrus demunis* (probably), from German east Africa, is credited by Stobbe with a Mallophagan parasite peculiar to it, *Trichodectes vosseleri* Stobbe.

The peccary, *Dicotyles tajacu* (family Dicotylidæ) of Central America and southwestern North America, has a Mallophagan species peculiar to it, belonging to the smaller of the two large Mallophagan genera, namely, Gyropus.

The dromedary, of north Africa and western Asia, and the bactrian camel, of central Asia, harbor a common sucking louse, *Hæmatopinus cameli.* A doubtful second species called *H. tuberculatus* (Neumann thinks it identical with *cameli*) has been recorded from a dromedary imported from India into Australia. The "South American camel," the llama, harbors an Anopluran species peculiar to it, and two Mallophagan species, *Trichodectes breviceps* Rudow and *T. inæqualemaculatus* Piaget. Although Rudow's species are often suspect, I have just had his *breviceps* from a llama of Peru (collector C. H.

T. Townsend). With these llama Mallophaga there is also a small Anopluran which I have not yet worked out.

The family Cervidæ is represented in the host list by about ten species. They are infested by three species of Anoplura, each peculiar to its host, and six species of Trichodectes (Mallophaga) of which *T. tibialis* is common to the roe deer of Europe and Asia Minor, an African *Capreolus*, and our own black-tailed deer of the western states. *Trichodectes longicornis* is common to the red deer of Europe and Asia Minor and the fallow deer of south Europe, Asia Minor and north Africa.

The giraffe (family Giraffidæ) harbors a sucking louse, *Linognathus brevicornis*, peculiar to it.

The great family Bovidæ, with its many buffalo, buck, sheep, goat and antelope kinds, is represented in the host list by five or six species of Bos, four African bucks, three or four sheep, the ibex, chamois and two or three goats, and five or six antelopes, or gazelles. The domestic ox, *Bos taurus*, harbors three species of Anoplura and one Mallophagan. Curiously, none of these species is recorded from any other Bos. On the other hand, the zebu, the Indian buffalo, and the American bison all have the same Anopluran species (and no other, nor any Mallophagan), while the yak of central Asia and the Kaffir buffalo each have an Anopluran peculiar to it. The four species of African reedbucks and duikerboks have, according to the records, each a peculiar species of sucking louse. These records need scrutiny. One of them is my own, but I had to describe the species without seeing the types of the others. The domestic sheep carries two Anopluran species and one Mallophagan. The latter occurs also on at least two wild species of Ovis, one of west Africa and the other of north Africa. The fat-tailed sheep has a record from German southwest Africa of a Trichodectes of its own.

The domestic goat harbors one Anopluran and at least one Mallophagan, the latter being common also to the Angora goat, the chamois, and a wild (?) goat of Guinea,

and a wild (?) goat of Java. A recent description of a second Mallophagan species from the domestic goat is not convincing. The chamois has also an Anopluran, but one, so far, peculiar to it. Three species of Gazella (or Antilope) have three species of Trichodectes, of which one is common to two host species, one of Arabia and Syria and the other of north Africa and southwest Asia generally. This same Trichodectes is also recorded from the roan antelope, *Hippotragus equinus*, of east central and south Africa. One species of Gazella carries an Anopluran peculiar to it, as does also *Tragelaphus gratus* of west Africa.

The order Carnivora is represented in the host list by eight families and a total of fifty-four species. Only one species of Anopluran, the common sucking louse of the dog (not found yet even on the wolf or fox, both of which have other records) is recorded from a Carnivore, outside of the two families Trichechidæ (walruses) and Phocidæ (seals and sea-lions). From these two families, on the other hand, only Anoplura are recorded.

The family Felidæ is represented by three species, the domestic cat, the California lynx and the tiger. The cat and lynx have a common Mallophagan parasite, *Trichodectes subrostratus* (and no other), while the tiger has a biting louse presumably peculiar to it. The description of this parasite is, however, very brief and unsatisfactory.

The family Viverridæ, mongooses, ichneumons and genets, is represented in the host-list by eight species, of which five are of the genus Herpestes. Two of these Herpestes species, one of southern Spain, north Africa and Asia Minor, the other of west, east and south Africa, harbor a common Mallophagan parasite. A record of the finding of *Trichodectes subrostratus*, the familiar biting louse of the cat, on *Herpestes pluto*, comes from the Kameroons (Africa). It is probably a case of straggling, the mongooses being common enough in gardens, and some of them fairly domesticated.

Of the family Canidæ there are records from eleven

species, including the domestic dog, a wild dog of South America, two wild dogs of Asia, two foxes, and a wolf. The domestic dog has a familiar sucking louse and is also credited with that problematical normal or straggling biting louse of a peculiar genus which I have referred to in my account of the parasites of the kangaroos *Trichodectes latus,* the common biting louse of the domestic dog, is also common to the wolf, *Canis lupus,* of Europe and Asia, and to the raccoon-like wild dog, *Nyctereutes procyonoides,* of Asia and Japan. The record of this last came, it must be noted, from the Berlin Zoological Gardens. There is no other record of commonness of parasite to two hosts in the family. The English fox has a single Mallophagan species, and the California fox has another. The dhole, a wild dog of the Himalayas, has a Mallophagan species, and the Magellan wolf of Patagonia has another.

The family Procyonidæ is represented in the host-list by two raccoons, the California ring-tailed cat, and two coatis of Central and South America, respectively. The two raccoons, *Procyon lotor* of North America and *Procyon psora* of California, harbor a common Mallophagan parasite. In addition a German record (from a zoological garden?) credits *Procyon lotor* with carrying also a Mallophagan which is the characteristic parasite of the badger. On the California ring-tailed cat, *Bassariscus astuta,* have been found two Mallophagan species, one of which is the characteristic parasite of the skunks of North and South America. The two coatis, *Nasua narica* and *Nasua rufa,* one of southwestern United States, Mexico and Central America, and the other of South America from the equator south, both harbor a common Mallophagan species.

The family Mustelidæ, comprising the badgers, weasels, martens, and skunks, an ill-smelling crew, offers no attraction to blood-sucking parasites, but is represented in the host-list by nearly twenty species from which Mallophaga have been taken. The Old World badger has

a characteristic species, *Trichodectes crassus*. The martens, weasels and ermine have also a characteristic species, *Trichodectes retusus,* which is recorded from the pine marten of Europe and northern Asia, the beech marten of the same range, still another Old World marten, the weasel of Europe and Asia, the ermine of north Europe, Asia and America, and the weasel and mink of North America, in all six or seven species of Mustela and Putorius of very wide geographic range. The skunks of North and South America have also a characteristic Mallophagan species, *Trichodectes nephitidis,* described by Osborn from the common North American skunk, *Mephitis mephitica,* taken in Nebraska. I have found this parasite on the western skunk, *M. occidentalis,* in California, and on *M. macrura* of Arizona. It has also been recorded from the spotted skunk, *Spilogale interrupta,* of the southern United States, Mexico and Central America, and I have examples from a "skunk" of Bolivia. It is also recorded from a Chilian Mustelid, *Galictis quiqui,* which ranges over South America from the River Plate south, and from another species of Galictis in Brazil. Finally, examples of this ubiquitous pest are recorded from *Helictis everetti* from North Borneo! The last record comes from Neumann, a very careful and well-informed student of the parasites, but his specimens were taken from a skin in the Museum of Natural History of Paris. The Old World otter, *Lutra lutra,* has a *Trichodectes* of its own, as has also an African otter, *L. matschiei,* and the North African *Zorilla lybica.* Mjöberg records a species of Boopia (typical kangaroo parasite genus) from *Lutra pruneri* of India. As the record is an extraordinary one, being the only case of a Boopia found outside of Australia or on a mammal other than a Marsupial, it is well to note the exact circumstances of the record. The parasites (several examples) were got by Mjöberg from the Hamburg Zoological Museum where they were ticketed as having been taken from a "soeben frisch angekommenes Thier" of the species *Lutra pruneri,* the animal having been received

from India. There are to be considered in connection with this extraordinary record, first, the possibility of an exchange of labels in the course of the several handlings of the Mallophagan specimens, and, second, the possibility of a favorable answer to the question: Is *Lutra pruneri,* which does not appear in Trouessart at all, only *Lutra lutra,* the common Old World otter, and was the specimen from which the Mallophagan came a resident in a zoological garden in which kangaroos or wallabies also lived, affording a bare chance of straggling? The similar aberrant records from dogs of the kangaroo parasite *Heterodoxus* have already been referred to.

The bears (family Ursidæ) have, so far, but one parasite record to present, a Mallophagan species, *Trichodectes pinguis,* having been described from the Thibetan bear, *Ursus thibetanus,* a century ago.

The walrus (family Trichechidæ) harbors a strange Anopluran parasite of species, genus and family peculiar to its host, as, indeed, might be expected of any ectoparasite daring enough to brave comrade life with walruses. Examples of the parasite have been taken from walruses from Spitzbergen, Frobisher Bay (Davis Straits), the Hamburg Zoological Garden, and I have recently had them from a "Pacific walrus" from "southeast of Siberia."

The family Phocidæ is represented in the host-list by at least five species of seals and sea-lions carrying an equal number of Anopluran species representing three different genera, all of them peculiar to the seals. A single parasite species, *Echinopthirius phocæ* has been repeatedly taken from the fur seal, *Proca vitulina,* from both Old World and New World shores. The harp seal of the Arctic is credited with the same parasite, as well as another. Hooker's seal of New Zealand and the Auckland Islands carries an Anopluran, *Antarctopthirius macrochir,* of species and genus peculiar to it, while the elephant seal of the south Pacific has another parasite also of genus and species peculiar to it.

The large order Rodentia is well represented in the

host-list, representatives of thirteen families, summing about sixty species, being listed. Both Mallophaga and Anoplura infest the rodents, but certain families are parasitized almost or quite exclusively by Anoplura, while Mallophaga are the only parasites of others.

The Sciuridæ (squirrels and spermophiles), for example, with a dozen host species, are parasitized by a dozen species of Anoplura with only a single Mallophagan record; and a single record under such circumstances is always suspect. There is little commonness of parasite species to two or more host species in this family. Osborn's *Polyplax montana* is recorded from the eastern and western North American gray squirrels, and his *P. suturalis* has been taken from two Spermophile species, both, however, of the same general range. The well-differentiated parasite genus *Acanthopinus* is represented by one species from the common Old World squirrel, *Sciurus vulgaris,* and another from the eastern gray squirrel of North America. These species, though close together, really seem to be different. In addition I have just found the Acanthopinus species of the eastern gray squirrel on Douglas's squirrel in California, and another (new) species on a California chipmunk. The only Mallophagan species recorded from a Sciurid is *Gyropus turbinatus* from the marmot, *Arctomys marmotta,* of the mountains of southern Europe.

From the beaver (family Castoridæ) a characteristic Mallophagan species, *Trichodectes castoris,* has been taken in America. The beaver, it may be noted, is the host of the only beetle (*Platypsylla castoris*) that has become a specialized permanent ectoparasite, passing its whole life on the body of its host.

The Old World dormouse (family Gliridæ or Myoxidæ) harbors a sucking louse, *Polyplax pleurophæa.*

The large family Muridæ, including the rats, mice, voles and lemmings, is represented by twenty host species well scattered over the world. There are twenty-two Anopluran species and two Mallophagan species in the parasite list for the group. Both of these Mallophagan

records are my own. One is a new species of Colpocephalum (exclusively a bird-infesting genus) from a "spotted rat," Uganda, Africa, sent me by Sjoestedt in a collection made by the Swedish Zoological Expedition to Kilimandjaro-Meru, Africa, in 1905–1906. It is undoubtedly a straggler from some bird taken at the same time. The other is a poor specimen of Trichodectes from *Mus rattus,* Canal Zone, Panama, sent me by Dr. Jennings. It may be a good record—or it may be a deceiving one. Both record and specimen need further scrutiny. It is, perhaps, important to note that two specimens of a wingless Psocid (Atropidæ) were sent with the lot labeled "parasites from *Mus rattus.*" It would be very interesting if we could know that these Atropids were really living on the rats, feeding on their hair or dermal scales. I have found Atropids in rats' nests and birds' nests living undoubtedly on the loose hairs, feathers and dermal exuviæ. It is my belief, based primarily on certain striking facts of morphology, that the Mallophaga are degenerate descendants of the Rsocidæ.[3] Of the murid Anoplura, two or three are common to several hosts, as the well-known *Polyplax spinulosa,* recorded from all over the world from the now cosmopolitan *Mus rattus* and *Mus decumanus,* as well as from *Mus sylvaticus* of Europe and north Asia, and *Mus alexandrinus* of south Europe and Asia Minor (perhaps only a variety of *Mus rattus*), and *Polyplax affinis* (perhaps only a variety of *P. spinulosa*) recorded from *Mus agrarius* of eastern Europe, and *Mus sylvaticus* of Europe and north Asia. *Polyplax* (*Hoplopleura*) *acanthopus,* the common sucking louse of the mouse has been taken from the now cosmopolitan *Mus musculus,* and also from *Lemmus torquatus,* the lemming of Arctic Europe, Asia and America, *Microtus agrestis,* the field vole of Europe, *Microtus arvalis,* another common vole of Europe and Asia, and *Microtus* sp. from Iowa, U. S. A. The water rat, *Hydromys chrysogaster,* of Australia, has a Polyplax species of its own as has also *Otomys bisulcatus* of south and central

[3] See *Psyche,* Vol. 9, 339, pp. 1902.

Africa, *Hesperomys leucopus* of North America, *Epimys aurifer* of the Malay Peninsula, *Gerbellus indicus* of northern India and Afghanistan, and *Holochilus sciureus* of Brazil and Peru. The common Old World mouse, *Mus minutus,* harbors three Anopluran species, while *Mus musculus* has but two. The Old World water vole, *Microtus terrestris,* has a parasite differing from the two infesting respectively the two Old World land species of Microtus.

In connection with this résumé of the Murid parasites, I may say that I have now in process of working over some two hundred vials of material collected last summer from California mammals, which is going to add many records to the Murid list of both hosts and parasites. It will also add numerous records for the squirrels and spermophiles (Sciuridæ).

The family Geomyidæ, gophers, is represented in the host list by three North American and one Central American species. The Mallophagan species *Trichodectes geomydis* occurs on all of these hosts. The North American hosts are *Geomys bursarius* (Iowa), *Thomomys bottæ* (California), *Thomomys bulbivorous* (California), and the one Central American host is *Macrotomys heterodus* (Costa Rica). *T. bulbivorous* may be a synonym of *T. bottæ.* In addition, *Geomys bursarius* has yielded an Anopluran species of genus and species peculiar to it.

The pocket rats, family Heteromyidæ, are represented by a species of Perognathus (Baja California), and *Dipodomys merriami* (Arizona). From both are recorded the same Mallophagan species, *Trichodectes californicus.*

The jerboa, *Dipus* sp., is the sole representative of the family Dipodidæ. From it is recorded an Anopluran species taken in Tunis.

The Octodontidæ are represented by three species parasitized by one Anopluran and three different Mallophaga. The three hosts are of three different genera, one with an African range, the other two of South America. The parasite species on each is peculiar to it. A third

record, crediting the characteristic *Trichodectes pilosus* of the horse to a coypou of South America (in the menagerie of the Jardin des Plantes in Paris), is certainly either a false record or one of rather extraordinary straggling. The two Mallophagan species from these South American tuco-tucos belong to the genus *Gyropus*, which is the Mallophagan genus especially characteristic of the related South American families, the Caviidæ (guinea-pigs), the Dasyproctidæ (agoutis), and the Chinchillidæ (chinchillas and vizcachas) (see following paragraphs).

The guinea-pigs and mocos (family Caviidæ) are represented by three species, and are strongly parasitized by Mallophaga. They have no Anoplura. The domesticated form, which is variously held to be a species distinct from any wild one now known, or a variety of the wild species, *Cavia cutleri*, harbors two well-known species of Gyropus, namely *G. ovalis* and *G. gracilis* (this latter is held by some students to be of distinct genus). In addition, Piaget has described a species of Menopon (bird-infesting genus) from it, and Paine and I have described another Menopon from it from collections we have had from Peru and Panama. We have also found this latter species on the wild guinea-pig, *Cavia cutleri*, from Peru, and from this host Paine has described a species of Gyropus peculiar to this host. From the Brazilian moco, *Kerodon moco*, has been recorded a variety of *Gyropus gracilis*, one of the familiar species of the domestic guinea-pig, as well as another species of Gyropus peculiar to the moco. Recently Cummings has described a new Mallophagan taken at Villa Rica, Paraguay, from the wild guinea-pig, *Cavia aperea*. For this new species he established a new genus called Trimenopon. As a matter of fact the species is so much like Kellogg and Paine's *Menopon jenningsi*, except for its markedly larger size, that I am not at all sure it should be added as a fourth guinea-pig parasite.

A single agouti, *Dasyprocta aguti*, from Brazil, represents the family Dasyproctidæ. From it have been described two species of Gyropus peculiar to it.

The chinchillas and vizcachas (family Chinchillidæ, or Lagostomidæ) are represented in the host list by two species, to which I can add another (perhaps two others) on the basis of material recently received from Dr. C. H. T. Townsend, of Peru. From *Lagidium peruanum* Gay long ago described a peculiar Gyropus, and I have specimens of a Gyropus which may or may not be different from Gay's species. His description is very meager. In addition I am about to describe, under the name *Philandria townsendi,* another species, representing also a new genus, specimens of which have been sent me by Dr. Townsend from the same host. Also in this Townsend sending are specimens of a small Polyplax species (Anopluran) from the same host.

The Cercolabidæ or Coendidæ, American porcupines, are represented in the host lists by five species, three of Central and South America and two of North America. They harbor no Anoplura, but are parasitized by two Mallophagan species, of which one, *Trichodectes setosus,* occurs on all the host species in the list. The second Mallophagan is a *Trichodectes* recently described by Stobbe from *Cercolabes nova-hispaniæ* of Mexico and Central America. The other South American host porcupines are *Coendu* (*Cercolabes*) *prehensilis* (northern South America) and *C. villosus* (Brazil). The North American hosts are *Erethizon epixanthum* (California) and *E. dorsatum* (Nebraska).

Finally the family Leporidæ, hares and rabbits, appears in the host list with six (perhaps only five) representatives, of which four, namely, *Lepus timidus,* of circumpolar arctic regions, *Lepus cuniculus,* native to Europe and north Africa but introduced over the whole world, *Lepus europæus* of Europe and *Lepus campestris* of western Canada and United States, harbor the same species of sucking louse, representing a genus peculiar to hares and rabbits. I must note that this species, *Hæmatopinus ventricosus* Denny, is commonly referred to as two species, of which one, *H. ventricosus,* is recorded from the American host species and *L. cuniculus,* while

the other, called *H. lyriocephalus,* is recorded from *L. timidus* and *L. europæus.* But Neumann, an exceptionally experienced student of the Anoplura, holds that the two species are one. A deer-infesting Mallophagan, *Trichodectes tibialis,* certainly a straggler, has been recorded from *Lepus europæus,* and another Trichodectes (a very old and uncertain record) from *Lepus cannabinus.*

The order Insectivora is represented by but two species, the mole, *Scalops argentatus,* of North America, and the shrew, *Sorex araneus* of Europe and Asia. Each harbors an Anopluran species, that of the mole being a curiously modified form and of species and genus peculiar to its host, while that of the shrew is of a species not found on other hosts.

The order Prosimiæ, the lemurs, presents a single record, that of a species of Mallophagan, *Trichodectes mjöbergi* Stobbe, described from the North Bornean *Nycticebus borneanus* (family Nycticebidæ).

The order Primates is represented in the host list by four families, the Cebidæ of the New World, the Cercopithecidæ, the single family of apes, Simiidæ, of the Old World, and the family of man, Hominidæ. The distribution of the ectoparasites of these groups is of unusual interest to the special student and will likely prove equally so to more general students.

The Cebidæ, platyrrhine, tailed, New World monkeys, are represented by two species, the spider monkey and one of the howling monkeys of Brazil, members of different genera, each with a Trichodectes species peculiar to it. In addition three species of Ateles, one of Mexico and Central America, another of Guiana and Brazil, and the third an undetermined species of the genus represented by a specimen in a traveling menagerie in Europe, have yielded three species of the Anopluran genus Pediculus, otherwise characteristic of man and the anthropoid apes. These three Pediculus species have been recorded and described by three different students of the group, all careful workers, and there can be no doubt of the generic reference. But it is to be noted that the specimens of all three

parasite species were obtained either from host skins in a museum (in one case the Zoological Museum of Hamburg, in another, the Berlin Museum) or from a live host in a menagerie. In no case, therefore, is the possibility of a straggling record wholly excluded, but the coincidence of three discoveries makes the records practically safe. Finally, in this connection it is to be noted (as I have already pointed out in a brief paper[4]), that, although Ateles is a tailed New World genus and presumably widely separated genetically from the anthropoids, Friedenthal has affirmed, on a basis of blood and hair comparison, that Ateles shows unmistakable differences from other tailed monkeys, and resemblances with the anthropoids, and he suggests that in Ateles we should see monkeys, which, in a certain sense, replace, in the New World, the anthropoids of the Old. It is, in any event, a strange thing that Ateles differs from the other Cebidæ and from the Cercopithecidæ as well, in not harboring the Anopluran genus Pedecinus to which all monkey-infesting Anoplura, except those of the simians, belong, but in actually harboring parasite species of the genus found elsewhere only on the simians and man.

The family Cercopithecidæ, catarrhine, Old World monkeys, is represented in the host list by a dozen species, from which one Mallophagan species, viz., my *Trichodectes colobi* from a guereza monkey, *Colobus guereza* var. *caudatus* (East Africa), and ten Anopluran species have been recorded. Of the Anoplura nine species belong to the genus *Pedecinus,* long recognized as the characteristic genus of the lower monkeys, as contrasted with the genus *Pediculus* characteristic of the anthropoid apes and man. For the tenth species, Fahrenholz establishes the new genus *Pthirpedecinus,* just as for one of the man-infesting species the separate genus *Phthirius* had to be established. There are several cases of the commonness of a single Pedecinus species to two or three hosts. *P. breviceps* Piaget is recorded from *Macacus silenus* of

[4] "Ectoparasites of the Monkeys, Apes and Man," *Science*, N. S., Vol. 38, pp. 601–602, 1913.

India, *Cercopithecus mona* of west Africa, and a third *Cercopithecus* skin in the Zoological Museum at Hamburg. *P. longiceps* Piaget is recorded from *Macacus cyclopis* of Formosa, *Semnopithecus maurus* var. *cristatus* of Borneo, and *Macacus cynomolgus* of the Malaysian region. *P. eurygaster* Gervais has been recorded from *Macacus sinicus* of India and on a macaque in the Zoological Garden at Sydney, and another in the Zoological Garden at Melbourne. A hamadryad (Paphio sp.) of north Africa has a Pedecinus species peculiar to it, as has a *trachypithecus,* of Malaysia, and the Barbary ape, *Macacus innuus,* of northern Africa and Gibraltar. The common *Macacus rhesus* carries one species of Pedecinus peculiar to it, and that single species of Phthirpedecinus already referred to. *Macacus silenus* also has recorded from it two species both belonging to *Pedecinus.*

The family Simiidæ, anthropoid apes, is represented in the host list by three species, namely, the chimpanzee and two gibbons. One of these gibbons is *Hylobates syndactylus* of Sumatra; the other is *H. leuciscus* of Borneo. A single species of *Pediculus* is common to them both, and is not elsewhere recorded. The chimpanzee has also a single species of *Pediculus* which is peculiar to it. No Pedecinus has been taken from a Simian.

Finally man, representing the fourth Primate family, Hominidæ, is the host of three notorious Anopluran species, two of which are species of Pediculus and the third the only species so far known of another genus, Pthirius. Neumann is inclined to see in *Pediculus corporis* only a variety of *Pediculus capitis.* All of these parasites are found on man in all parts of the world. Some curious variations among the parasite individuals are shown, perhaps the most curious being a plain tendency to a darker coloration of the individuals occurring on the bodies of men of the dark-skinned races. In my brief discussion elsewhere, already referred to, I have noted the interesting significance of this possession by man and the anthropoid apes of a common genus of Anopluran parasites, while the parasites of the lower monkeys belong to

a well-distinguished other genus. There is no doubt that the close physiological fitting of parasites to host makes their host distribution significant of genetic or "blood" relationship, and this commonness of one type of parasite to man and the apes, and its limitation to these hosts, and replacement on the lower monkeys by another parasitic type, is an added indication of the actual blood-likeness of the Simians and man, a likeness apparently greater than that between the Simians and the lower monkeys.

III

In the light of the plain statement in part I of this paper of my belief gained from a study of the distribution of the bird-infesting Mallophaga, to the effect that the host distribution of the permanent wingless ectoparasites of birds is determined more by the genetic relationships of these hosts than by geographic relationships or any ecological condition, and the corollary of this, which is that the distribution of the parasites may therefore often have a valuable significance as to the genetic relationships of animals whose genealogic affinities are in process of ascertainment, and in the light of the facts of distribution for the mammal-infesting Mallophaga and Anoplura as just set out in part II of this paper, I hardly need to do more, in conclusion, than to point out that the distribution conditions exhibited by the mammal parasites, even in the face of the meager knowledge that we yet have of the mammal-infesting forms, clearly, on the whole, confirm this thesis. In fact, considering how few mammal-infesting parasite species we yet know, it is surprising how repeatedly the commonness of parasite species to two or more related, although geographically well separated, host species, is illustrated. All through the order from Marsupials to Quadrumana this condition is again and again exemplified. I am then, naturally, made more certain of the essential truth of the thesis, and can the more strongly recommend the attention of systematic zoologists to that practical application of it, which I have stated in the form of a corollary.

REGENERATION, VARIATION AND CORRELATION IN THYONE

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It is well known that many Echinoderms possess a remarkable power of regeneration, and the results given here show some interesting phases of this process in *Thyone briareus* (Leseur). The problem was suggested a few years ago in connection with class work in the Marine Biological Laboratory at Woods Hole, Massachusetts. There it is a common practise for students who are taking the invertebrate course to keep aquaria in which are placed specimens brought in from various collecting trips in the vicinity. Students are encouraged to study the behavior of these animals, but their enthusiasm for collecting frequently causes them to overcrowd their aquaria, with disastrous results. After collecting Thyone, especially if they are kept in stagnant water, the student is frequently amazed to find one or more of his specimens that have undergone evisceration. In this process the animal not only loses the principal feeding organs, the tentacles, and the entire digestive system, consisting of the esophagus, stomach and intestine; but it also throws out a whole series of organs surrounding the esophagus including the circlet of calcareous plates, the nerve ring forming the central nervous system, the portion of the water-vascular system known as the ring canal with its attached stone canal and Polian vesicles, and the muscles which serve as retractors for the set of organs surrounding and attached to the esophagus. We shall refer to these muscles as retractors of the esophagus.

The remainder of the animal after evisceration consists, principally, of the dermo-muscular integument, the

cloaca with its attached respiratory trees, the single gonad, the radial canals of the water-vascular system and the major portion of the dorsal mesentery by which the intestine was suspended. Since this part of the animal continues to give reactions, the student invariably raises the question, "Can Thyone regenerate the lost parts?" This question was the starting point of the following investigation. The work had not proceeded far when it was discovered that important individual differences occurred, and the question became, "To what extent, or how completely, may these individual variations be reproduced in the process of regeneration?" Curiously enough, the most important differences between individual Thyone involve structures which help to form the radial symmetry of the animal. Consequently the problem has a bearing on the phylogeny as well as the ontogeny of Thyone.

In general, the results show that regeneration of all lost organs may occur and that there is a decided tendency to even reproduce individual variations. It was found that the Polian vesicles varied greatly in number, size and location. The retractor muscles in a single radius were single or multiple, and for each individual this variation was closely correlated with a corresponding variation in the number of Polian vesicles. Whether one or more Polian vesicles are present, there is a strong tendency for these to occur on the left side of the animal, a fact which undoubtedly has a phylogenetic significance. A more complete statement and a discussion of these results will be given in the following pages.

General Structure of Thyone

Thyone is functionally a bilateral animal. It has anterior and posterior ends, dorsal and ventral surfaces, and consequently right and left sides. The external opening of the genital duct is located near the anterior end in the mid-dorsal region. The structure and arrangement of the tentacles is alike on both sides of the animal. Even

the feeding reactions, as Pearse has pointed out, indicate a bilateral type. The single genital gland is median in position; the genital duct and the stone canal are in the median dorsal mesentery; a part of the intestine and the stomach are supported by the same structure. The respiratory apparatus is also a bilateral structure, one branch arising from each side of the cloaca.

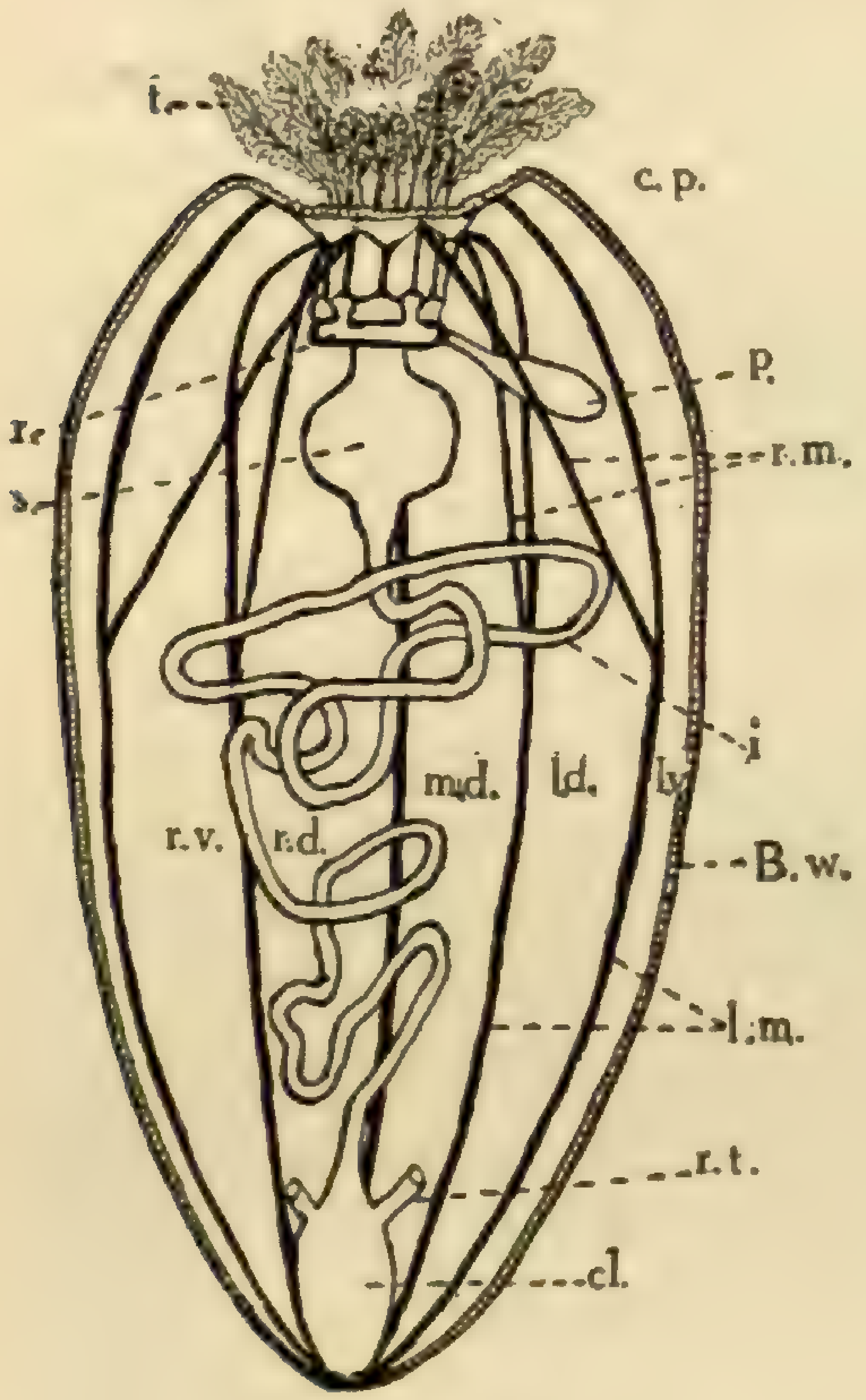

Fig. 1.

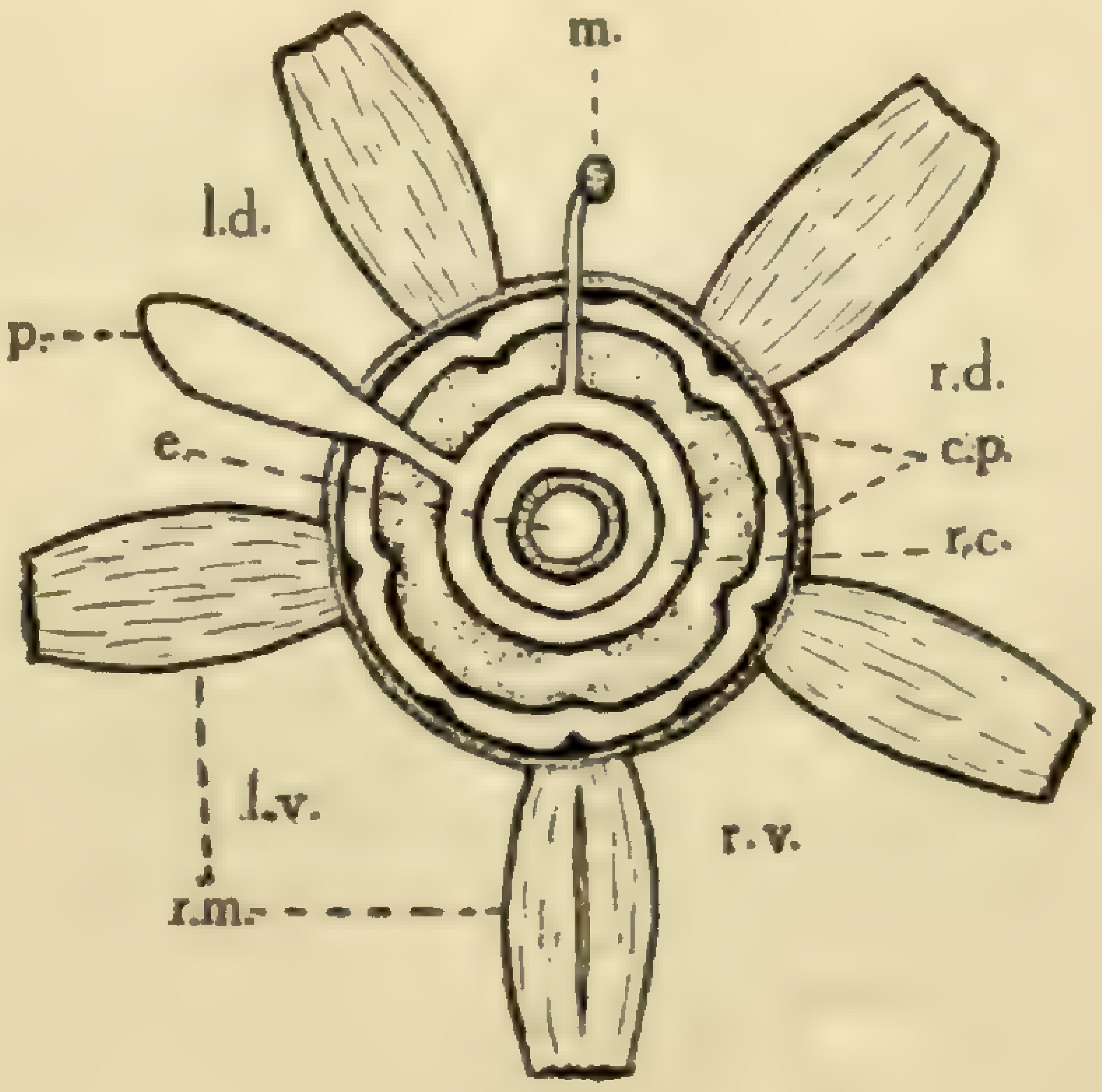

Fig. 2.

Fig. 1. A Diagrammatic Drawing from a Dissection Made by Taking a Longitudinal Cut in the Body Wall a Little to the Left of the Mid-ventral Line. Shows the arrangement of the chief organs concerned in evisceration and subsequent regeneration. *B, w.*, body wall; *cl.*, cloaca; *c. p.*, calcareous plates; *i.*, intestine; *l.* m., longitudinal muscles; *p.*, Polian vesicles; *r.*, ring canal; *r. m.*, retractor muscles; *r. t.*, base of respiratory tree; *s.*, stomach; *t.*, tentacles; *m. d.*, mid-dorsal; *l. d.*, left dorsal; *l. v.*, left ventral; *r. d.*, right dorsal, and *r. v.*, right ventral, interradial spaces.

Fig. 2. A Diagram to Show the Relation of Radial to Bilateral Symmetry. The esophagus (*e*) is shown in cross-section, cut just anterior to the stomach, and the view looks toward the anterior end. *M.*, madreporite; *r. c.*, ring canal. Other letters as in Fig. 1.

Notwithstanding this general tendency toward bilateral symmetry, the most conspicuous differences between individuals involve structures of the radial type. Fig. 1 is a diagrammatic drawing of a dissection to show the general

arrangement of some of the more important structures studied in this experiment. The dissection was made by making a longitudinal cut in the body wall a little to the left of the mid-ventral line, and then pulling the flaps apart and pinning the animal down on its dorsal surface. The Polian vesicle is shown attached to the ring canal in the position where it is usually found when only one is present, that is in the left dorsal interradial space. It will be noticed that the retractor muscles are simply branches of the longitudinal muscles, and hence are radial in position. At the time of evisceration the body wall breaks a short distance posterior to the tentacles, the retractor muscles separate at the point where they join the longitudinal muscles and the intestine breaks off just in front of the cloaca.

A better understanding of the radial type of structure will be gained by a reference to Fig. 2. This figure is a diagram to show the relation of the radial to the bilateral symmetry. The dorsal side of the animal is represented toward the top of the page, the esophagus appears in cross-section, cut just anterior to the stomach, and therefore one is looking forward to the other organs shown. The retractor muscles, showing the position of the radii, are much contracted and thickened, a condition in which they are usually found after evisceration. The stone canal ending in the small madreporite is located in the mid-dorsal interradial space. Passing around in a clockwise direction, the other interradial spaces are designated as right dorsal, right ventral, left ventral and left dorsal. Polian vesicles may be found in any of the interradii except the mid-dorsal space which always bears the stone canal. Although only one Polian vesicle is represented in this figure, the mid-ventral retractor muscle is shown double, a split condition which is characteristic when two or more Polian vesicles are present. This description will be sufficient to show the general relation between the radial and the bilateral symmetry.

Evisceration

Only one method of producing evisceration was used. By placing a number of Thyone in a small aquarium of stagnant sea water, the supply of oxygen is soon exhausted. The animals become greatly distended, they crawl up on the sides of the aquarium when possible, and extend the siphon toward and frequently above the surface of the water. All of their behavior, including the pumping of the siphon, indicates that respiration is inadequate. In the course of a day or two the water becomes very foul; soon some of the Thyone will eviscerate, and a considerable percentage will do so as conditions grow more unfavorable. Many, however, resist the unfavorable surroundings and will not eviscerate though kept for several days in foul water. But if the aquarium is now placed where it will have a continuous stream of water and air bubbles passing through it, the behavior of the animals is somewhat different. They then tend to contract to a minimal size, and sometimes assume a volume not more than one fifth to one seventh of their maximum distention. The respiratory movements are practically discontinued; the animal seeks a position as close as possible to the side and bottom of the aquarium. Contraction does not always take place immediately. To my surprise, after several hours I found Thyone which had resisted the previous unfavorable conditions now discharging their viscera. After remaining two or three days in the running water, and the animals had apparently become adjusted to this condition, I again set the aquarium to one side partly filled with water. Then, by repeating the conditions of the first experiment, as the water became foul several more of the holothurians apparently found life too strenuous to further retain their internal organs. When the remainder of this lot of Thyone was returned to running water, and again to stagnant water, a few additional individuals underwent self-mutilation. Out of a total of sixty-one specimens used in this lot forty of them eviscerated. That is, autot-

omy occurred in at least sixty-five per cent. of Thyone, under the conditions described. Probably one reason why this process did not occur in a still larger number is that some animals occupied more favorable positions in the aquarium. A discussion of the cause of evisceration will be given later.

When evisceration occurs it is sometimes hard to see just how the process takes place. Pearse ('09) ascribes the process to a "structural accident"; that is, it is due to a powerful contraction of the circular muscles at a time when the calcareous ring is well forward. "But if the tentacles are extended," he says, "and the calcareous ring is pushed forward a break may occur at *b*" (a point in his Fig. 2 where the body wall joins the calcareous ring) "as a result of the strong contraction of the circular muscles at that point, and the visceral organs are forced out. . . . Whether this autotomy takes place or not depends upon the breaking of the inner branch of the longitudinal muscle bands, whose normal function is to retract the calcareous ring. When the strain brought about by the contraction of the circular muscles becomes too great these inner bands are torn asunder, usually at the point *x*" (inner end of the retractors of the calcareous ring). While it is true that muscular contraction and consequent pressure undoubtedly plays a prominent part in the process, close observation has convinced me that this is not the only factor causing evisceration. Upon several occasions I have watched carefully the breaking of the body wall near its attachment to the calcareous ring, and while there are times when the pressure appears to be strong, especially when the animal is being irritated mechanically, there are other times when the skin appears to "melt away" or separate with very little or no pressure present. Indeed, after the skin once breaks at one side and the viscera escape through the opening, the pressure is relieved. But one may observe that the skin continues to break until the calcareous ring is entirely separated. This, of course, would not happen if the process

depended entirely upon an accidental structural defect. Another thing noticed is of interest in this connection. When splitting open the body wall of an animal that was eviscerating, and thus relieving any internal pressure that might be due to contraction of the circular muscles, some of the retractors were seen still attached to the longitudinal muscles. Under these conditions it would not be possible for the retractors to exert any pull against the pressure produced by the circular muscles, yet the retractors were observed to constrict off or break away from the longitudinal muscles by what appeared to be purely a local disturbance. It is hard to see how this could happen, or how the skin continues to separate around the calcareous ring after the first break is made, if the process of evisceration depends solely upon the breaking of retractors and internal pressure. Indeed, the view that local changes take place in the tissues is supported by other facts. Leptosynapta, if left in stagnant water or under other favorable conditions, undergoes repeated autotomous fission as the result of local constrictions, and Pearse states that autotomy depends upon the presence of the anterior portion of the body, and presumably upon the presence of the circumoral nerve ring. However, he found in Thyone that highly irritating substances like acetic acid and clove oil did not produce ejection of the viscera.

Nor were drugs like codene and atropine, which cause violent peristaltic waves of contraction to pass over the body, any more potent in inducing autotomy. The same may be said of sodium chloride, atropine and clove oil, although the injection of any of these substances was often followed by a waving of the oral tentacles to perform feeding movements, thus bringing about favorable anatomical relations for autotomy.

These results would indicate that the nervous system is not primarily involved. Certainly the ejection of viscera may occur in Thyone without any visible external stimulus.

The parts eviscerated in Thyone have already been

mentioned. However, sometimes evisceration is incomplete, as the following examples will show. On the morning of August 4, a Thyone, which we shall later speak of as individual *H,* was found eviscerating in an overcrowded aquarium jar. While the process usually requires only a few seconds, or at most a few minutes, the intestine in this case was not completely thrown out until two or three hours later. This animal lived until killed at the end of twenty-one days. In the afternoon of the same day on which individual *H* eviscerated, another Thyone was found with the process only partially complete. Five hours later the intestine was still retained, and scissors were used to cut it off at its anterior end near the stomach. Though this Thyone received equally good care it died at the end of two days without further evisceration. A third specimen was found incompletely eviscerated on the above date, but it was allowed to stand until the next morning; at this time the injured end was open, the intestine was still within the body cavity and a part of one of the branchial trees was protruding. The intestine was pulled out and broken off, after which the branchial tree was retracted and the injured end partially closed. This animal also died at the end of two days. A fourth Thyone was seized and by squeezing was forcibly caused to throw off the usual parts except the following: a part of the stomach, most of the intestines, and some of the retractor muscles which had broken off near their esophageal end. The next morning it had expelled the remainder of the stomach and intestine, two complete retractor muscles, and some débris which had escaped from the intestine into the body cavity. The anterior end of the part remaining appeared ragged and imperfectly closed. It died on the third day. It is probable that the two retractor muscles last expelled were broken off at their posterior ends by local constriction, not when the body was under pressure. A fifth animal, which we shall designate as individual *M,* was found partly eviscerated

late on the afternoon of August 6. The next day it still retained the stomach and intestine and at noon the digestive tube was clipped off with scissors in the region of the esophagus. Nothing peculiar was noted in its behavior until four days later, August 11, when it discharged the remainder of the digestive tube. It lived and was killed at the end of eighteen days. These results are typical. The animal dies unless it is itself able to eliminate all organs concerned in the process of evisceration, and therefore regeneration does not occur unless all these organs are eliminated.

The eviscerated animals show comparatively a low degree of mortality. In an attempt to raise twenty-five mutilated Thyone seven died; three of these were unable to complete the process of evisceration as described above, and two more, since they lived for fourteen days, probably owe their death to other causes. The sixth specimen to die lived three days and had been slow in eviscerating. The seventh did not receive the best of care and died after three days. So considering the amount of injury the mortality is extremely small where proper care is taken and evisceration is complete.

It will not be inopportune to describe the subsequent behavior of the different parts after evisceration. The parts expelled lie on the bottom in a more or less inactive condition until they die, which happens usually in the course of a few hours. At first the tentacles frequently expand and contract. They are highly sensitive, as one would expect, and if touched withdraw quickly into the esophagus and at the same time the retractor muscles will undergo strong contraction. By supporting these parts near the surface of the water, so as to insure plenty of oxygen, an attempt was made to keep them alive. In some cases the parts remained alive for two or three days, so this experiment appeared to be partially successful. Death is probably due to the direct exposure of tissues to the sea water and to the attacks of minute organisms. The dermo-muscular portion of Thyone is

much less sensitive than the expelled portion, just after evisceration. This is due to lack of a central nervous system.

Behavior During Regeneration

After evisceration each specimen was placed in a separate jar of fresh sea water. The injured end of the body turns in and closes up tightly, and the entire body is somewhat smaller than before evisceration. Respiration is slower and not so vigorous. If the water is stagnant, within a few hours the animal usually climbs up on the side of the aquarium by means of its tube feet. This part of the animal therefore is capable of responding to a lack of oxygen, and the reaction is independent of the central nervous system.

The observations upon the following individual, referred to in my notes as Thyone *A*, will serve to illustrate the general behavior during regeneration:

July 14, A.M.—Animal eviscerated itself in the usual way. In the afternoon it climbed up on the side of the jar and clung there evidently for the purpose of respiration.

July 15–16.—Acts as on the afternoon of the fourteenth. Keeps closed and well contracted at the injured end. Entire body somewhat smaller than before evisceration, due in part to organs lost. Respiration slower and not so vigorous as normal.

July 17.—In the afternoon, after water was changed, Thyone took up position on the sand against the side of the jar farthest away from the source of light.

July 18.—The next morning it was half buried in the sand in same position, with a few pieces of débris pulled over it. Remained so all day.

July 23.—For some two days it has been slowly burrowing down until only the two protruding ends of the body can be seen. When a piece of débris that was being held over a part of the anterior end was touched, this end retracted below the surface and the posterior end withdrew until it could scarcely be seen. Later the posterior end retracted when the shadow of my hand passed over it, the hand being held about one foot away. The uninjured animal is even more sensitive to shadow. The respiratory movements are growing stronger.

July 28.—For the past two or three days the Thyone has been slowly moving through the sand in a posterior direction without uncovering itself.

August 2.—It is now oriented with respect to the direction of the light and has reached probably the darkest portion of the jar.

August 7.—Has advanced still farther. Came about half way out of the sand to do this.

August 8.—Reacts quickly to shadows by withdrawing, and to jarring the table. Evidently is recovering its normal behavior.

August 10.—Has again come up about half way out of the sand. Reacts quickly to shadows as before.

August 11.—Came entirely out of the sand. Spent the day on the sand or on the side of the jar. Appeared restless.

August 12, 4 P.M.—Has been clinging to the side of the jar and moving about more or less all day. Respiratory movements are strong and apparently normal. Has just now expanded the anterior end sufficiently for me to see the new growth of tissue formed around a pentagonal opening. Fifteen minutes later it was observed to extend a set of minute tentacles and go through feeding movements. The tentacles appeared to be slightly more than three eighths of an inch in length. Its behavior continued apparently normal until it was killed twelve days later.

The actions of other Thyone were studied under the same conditions, and we shall now give a general summary of their behavior during regeneration. The earliest reactions after evisceration take the form of contractions resulting in the closure of the wound, and movements in response to lack of oxygen. If the oxygen supply is sufficient Thyone will draw itself closely into the angle between the side and bottom of the aquarium, or if the supply is deficient, it clings close to the side of the jar near the surface. In from three to seven days an instinct to burrow usually asserts itself. There is a tendency for the body to contract very noticeably at this time, and the whole organism becomes rather inactive. This condition is probably necessary for the formation of new tissue. Pearse makes the statement that in burrowing the normal Thyone will cover itself in from two to four hours. My observations on the mutilated animals indicate that they require from twelve to twenty-four hours, in one case forty-eight hours, to complete the reaction. The process frequently stops for some hours and occasionally is never completed. In the Thyone de-

scribed above the animal did not begin to orient itself with respect to the source of light until about the twelfth day, but in another case the response took place on the second day, which shows that this reaction does not depend upon the central nervous system. It should be stated that normal Thyone similarly placed were used as controls. Thyone *A* was quite sensitive to shadows and to touch on the ninth day, but it reacted more quickly on the twenty-fourth day both to shadows and to mechanical disturbances. Whether this was due to the regeneration of a new central nervous system, or to a more highly developed specialization of function in the old tissue, I am unable to say. It is quite possible that both factors were involved. Respiration is undoubtedly correlated with the activity of the animal, and feeding movements do not occur until the regeneration of all organs is well established, at about twenty-seven or twenty-eight days.

The internal changes that take place during regeneration were studied in animals that were killed at different stages in the process. Thyone *N* was killed nine days after self mutilation. At the injured end there was a very small plug of tissue representing the newly formed esophagus; a thread-like continuation of this tissue, the beginning of a new stomach-intestine, was also seen in the mesentery. The calcareous ring and the ring canal were not clearly defined. Another Thyone was killed at about the same age after evisceration; India ink was injected into the cloaca and into the opening at the anterior end in an attempt to demonstrate a cavity in the newly formed thread-like, stomach-intestine. The results were negative and the esophagus was found to be tightly closed. However, the interesting observation was made that the anterior end of *each of the longitudinal muscles had split off a very slender branch to form a new retractor muscle* (see Fig. 3). These newly formed retractor muscles were not more than one fourth inch in length; their anterior ends were attached in a normal position around the esophagus, but their posterior ends

were attached only a short way back, much in front of the position of attachment of the full-sized retractors. In another animal killed when a day or so older, the same conditions held with reference to esophagus, stomach and intestine. At least three of the radial canals belonging to the water vascular system had branched and connected at their anterior ends in such a manner as to form a part of a new ring canal (cf. Fig. 4). I was unable to find the rest of the ring-canal and perhaps it was not yet complete.

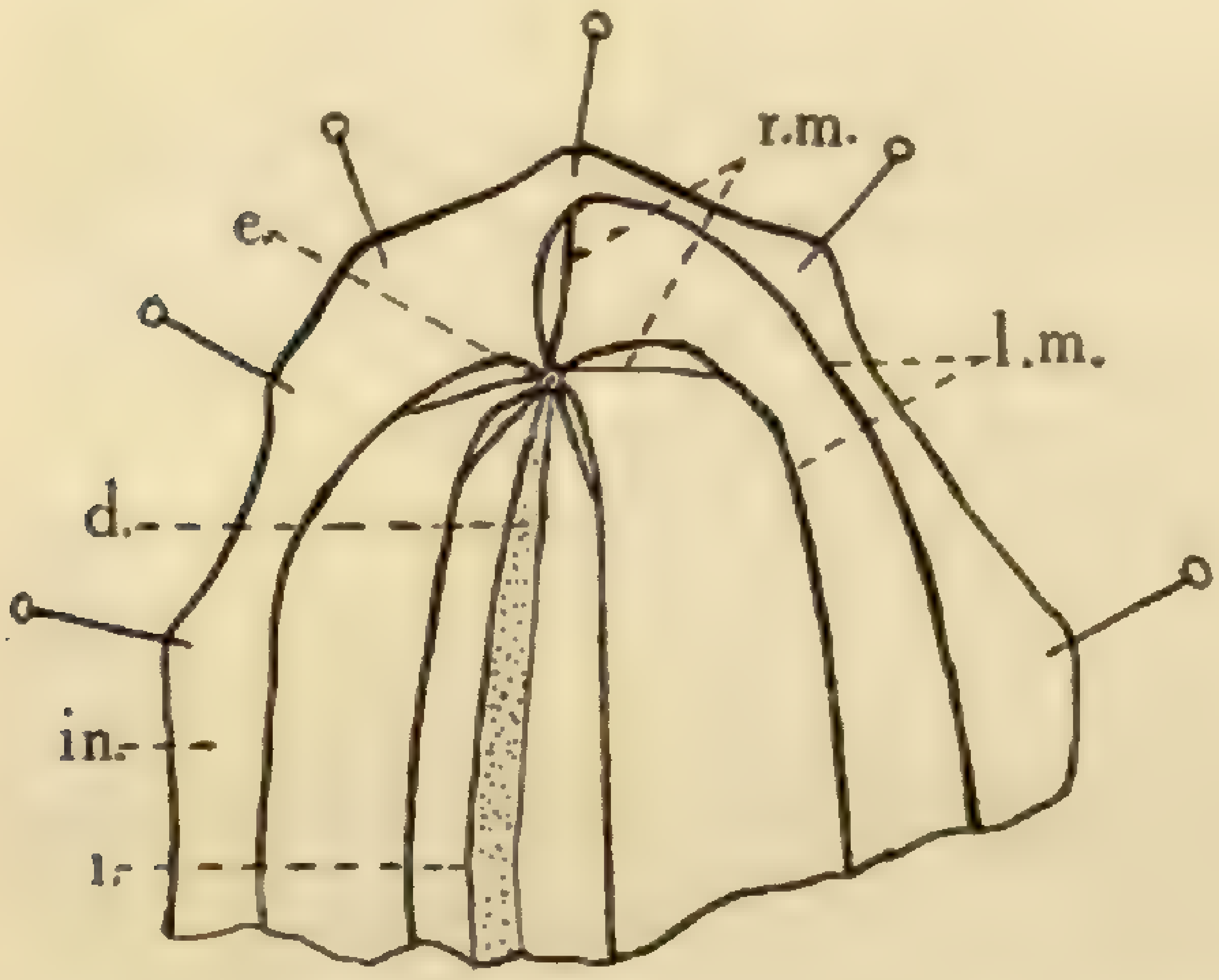

FIG. 3.

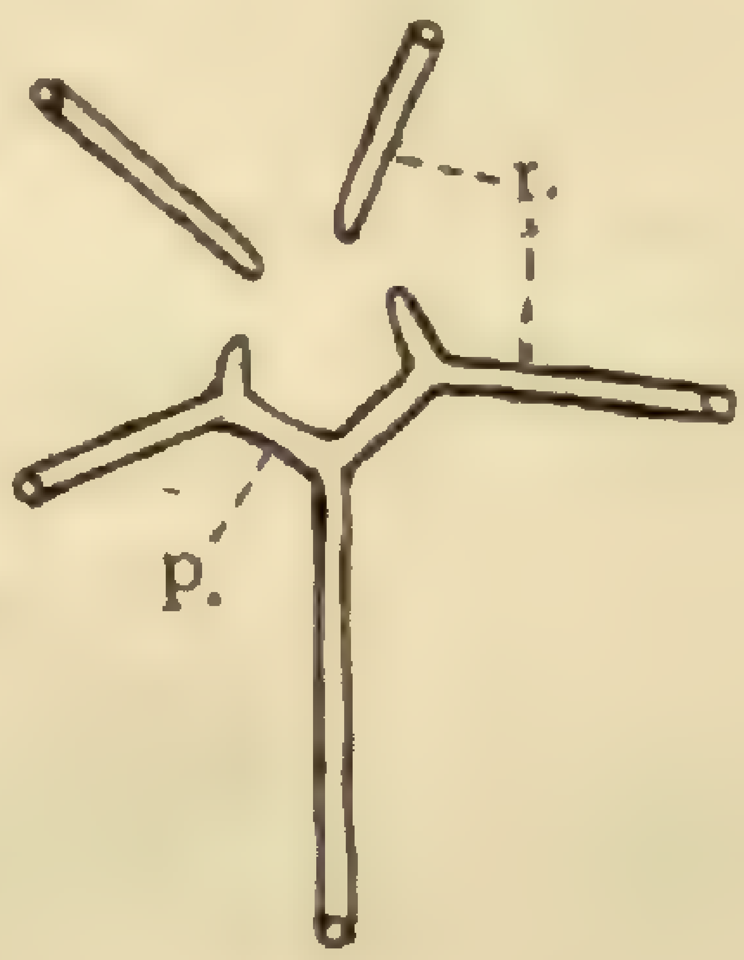

FIG. 4.

FIG. 3. DIAGRAMMATIC DRAWING TO SHOW THAT IN REGENERATION THE RETRACTOR MUSCLES (*r. m.*) ARISE BY SPLITTING OFF FROM THE LONGITUDINAL MUSCLES (*l. m.*). Dissected a little to the right of the mid-ventral line; *d.*, dorsal mesentery suspending the intestine (*i.*); *in.*, integument; *e.*, region of esophagus.

FIG. 4. TO SHOW THE DEVELOPMENT OF THE PENTAGONAL CANAL IN A THYONE ABOUT NINE OR TEN DAYS AFTER EVISCERATION. *r.*, radial canal; *p.*, pentagonal canal. The anterior ends of the radial canals fork dichotomously, and these branches anastomose to form the canal which later assumes a circular shape around the esophagus.

Thyone *F*, which was killed twelve days after evisceration, showed minute calcareous plates which formed a very small esophageal ring not more than one millimeter in diameter. The esophagus continued posteriorly in the form of a small tube, the stomach-intestine, which was suspended in the dorsal mesentery. This new digestive tube was about 0.5 millimeter in diameter and contained small, colored, movable particles that could be seen with the unaided eye. The ring canal was completely formed.

Another specimen, Thyone *O*, died at the end of four-

teen days and was in bad condition when examined. The stomach had begun to expand and retractor muscles were present. Probably owing to the condition of the specimen, no calcareous ring, ring canal, or Polian vesicle could be found. Another individual killed at about fifteen days showed the stomach slightly enlarged, and the intestine, retractor muscles, calcareous ring, tentacular canals, and ring canal well formed. Two small Polian vescicles each about one millimeter in length were present. The position of the new intestine was described in my notes as follows:

From the stomach the intestine follows the ventral edge of the dorsal mesentery, lying ventral to the gonaduct. At the gonad it turned ventrally with the mesentery and then forward for about one half inch to the left interradial space; here it turns rather abruptly backward, continuing in the mesentery below the left branchial tree to the anterior ventral part of the cloaca.

At a little later stage in another specimen the intestine passed from the left ventral interradial to the right ventral interradial space; then posteriorly and again to the left, following the ventral radial mesentery to the anterior ventral side of the cloaca.

We see from the preceding description that all important organs have been reproduced in form though not in size, before the end of the fifteenth day. The first madreporite with its tiny stone canal was found some eighteen days after mutilation. Twenty-one days after evisceration in one specimen the calcareous ring was about three millimeters in diameter and the ampullæ at the bases of the tentacles were well developed. Within a week after this time the regenerating animal begins active feeding. Thyone *A*, killed at 41 days, was practically a normal animal both in behavior and appearance, except for the fact that the regenerated organs had not yet reached full size. The stomach was about one third normal size, but the Polian vescicles were better developed. The intestine contained a small amount of food material and was nine or ten inches in length; most of this growth had

taken place posterior to the gonad. It was held in position as previously described and had several additional coils.

Individual Variations

To all outward appearances any two Thyone are as much alike as two peas. It was not until the internal organs were studied that important differences were ob-

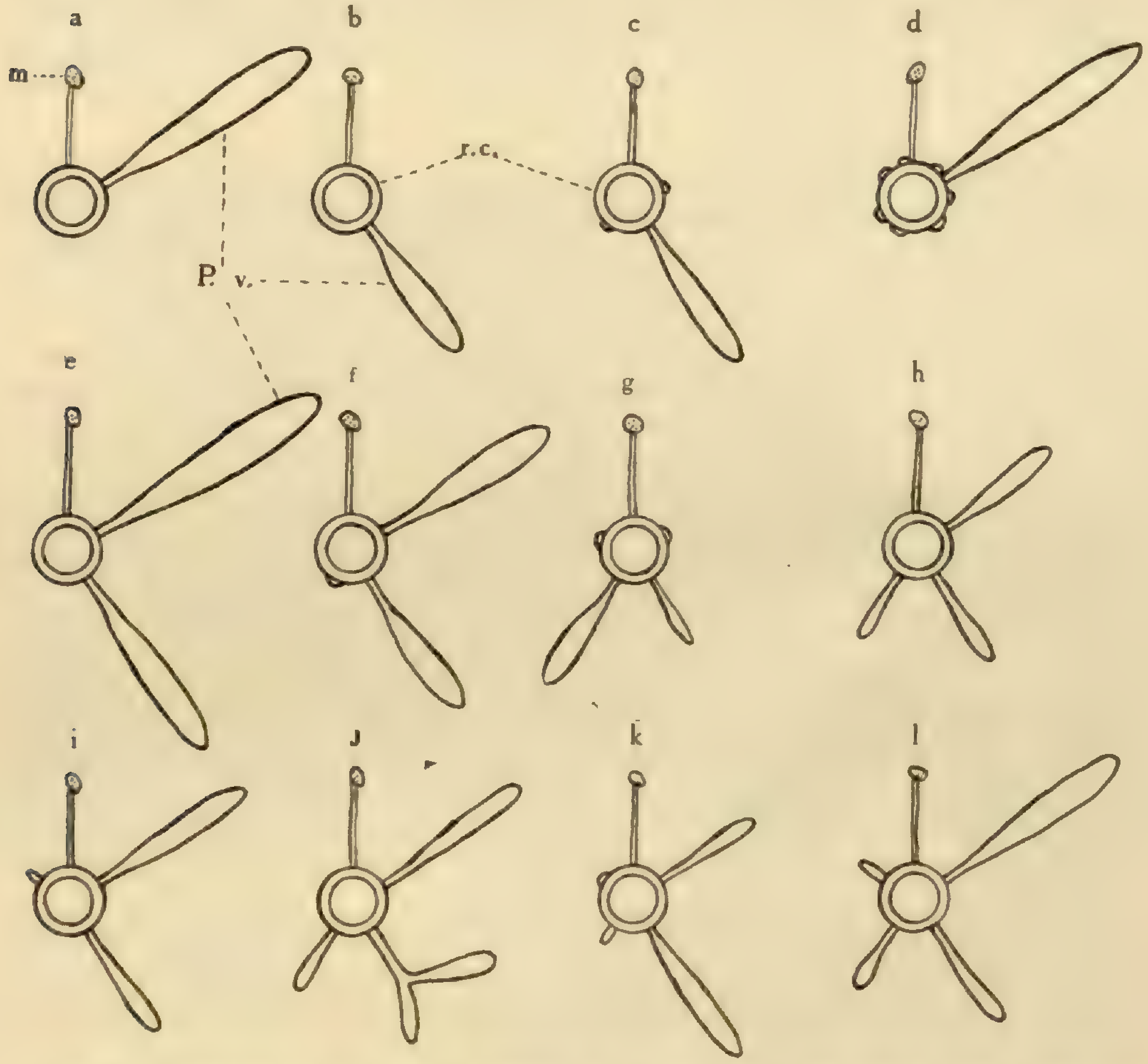

Fig. 5. Diagrams to Show Variation in Position and Size of the Polian Vesicles. *P. v.*, Polian vesicles; *m.*, madreporite; *r. c.*, ring canal; *a-d*, with one Polian vesicle, *e-g*, with two; *h-k*, with three, *l.*, with four; *c.*, *d.*, *f.*, *g.*, *k.*, with additional rudiments of these vesicles; *j.*, with a branched vesicle.

served. While there are numerous minor differences, the most conspicuous variations are found in the number, size and location of the Polian vesicles (cf. Fig. 5), and in the number and arrangement of the retractor muscles. On account of the radial structure of Thyone not more than four Polian vesicles are present, since

a homologous structure, the madreporite and its stone canal, occupies the dorsal interradial space. The number of vesicles varies in fact from one to four. By a reference to Table I, it will be seen that out of 77 individually examined, 41 had one, 20 had two, 14 had three,

TABLE I

To Show the Number of Polian Vesicles Present in a Given Number of Thyone. Also to Show their Location in the Interradial Spaces, with Reference to the Bilateral Symmetry of the Animal

Number of Polian Vesicles	Number of Individuals Examined	Left Dorsal	Left Ventral	Right Ventral	Right Dorsal
1	41	38	3	0	0
2	20	17	19	3	1
3	14	14	15	12	1
4	2	2	2	2	2
Totals..........	77	71	39	17	4

and 2 had four Polian bodies. If one is to test the matter of regeneration, of course it is important to know whether the variations or individual peculiarities will be accurately reproduced. Another striking characteristic comes out when we note in the same table the location of these organs. Of the forty-one individuals which had a *single Polian vesicle, all were on the left side of the animal,* and 38 were in the left dorsal interradial space. In twenty specimens with two Polian bodies each, 36 were on the left side and only four on the right side of the body. A similar asymmetrical distribution of these parts was found when three Polian bodies were present. In one specimen, however, two vescicles were found in one space, the left ventral interradius, the only instance of this kind observed; on account of this doubling, the right side lacked one of the number to which it was entitled in the table. Where four Polian bodies are present the arrangement is, of course, symmetrical on both sides. Still another interesting fact comes out when we examine the totals in the last line. Out of the 77 individuals, 71 had a Polian vesicle in the left dorsal interradial space, 39 vesicles were found in the left ventral,

17 in the right ventral, and only 4 in the right dorsal space. That is, the total number on the left side compared with the total number on the right side bears the ratio of 110 to 21. Not only is there this tendency for the vesicles to be more abundant on the left side of Thyone, but the totals show that *the chances of a given Thyone having a Polian vesicle in any given interradial space decreases in a counter-clockwise direction*, beginning with the left dorsal interradial position. Coinciding with the number of individuals examined, the maximum number of chances is found in the mid-dorsal interradius, where the stone canal is always present. That is, the stone canal with its madreporite is a more fundamental and stable structure than each or all of the vesicles.

The conditions are none the less interesting when we compare the Polian vesicles with reference to size and location, as will be seen from the examination of Table II. The Polian vesicles are here divided arbitrarily into three groups, designated as large, medium and small, and their respective locations are shown. In addition some Thyone had the rudiments of other vescicles, each too small to be considered a distinct pouch. These are designated in the table as a "rudiment." It will be noticed that all of the large, and most of the medium-sized vesicles are on the left side; that all the small ones, and most of the rudimentary ones are on the right side. The table as a whole shows that not only does the number of Polian vesicles diminish in a counter-clockwise

TABLE II

To Show the Polian Vesicles with Reference to Size and Location

Size	Left Dorsal	Left Ventral	Right Ventral	Right Dorsal	Total
Large.......	56	17	0	0	73
Medium.....	17	22	5	1	45
Small.......	0	0	10	3	13
Rudiment...	2	1	5	7	15
Total.......	75	40	20	11	146

direction, but their size diminishes following the same law. These facts appear significant and without doubt are suggestive of ancestral history.

If it is true that the radial symmetry of Echinoderms is to be ascribed to a fixed stage in their ancestral history, we are led to suppose that the point of attachment was on the right side of an originally bilateral animal. The life history of Pentacrinus, the larval organ of Asteroidea, and a great many anatomical and embryological facts support this view. While it is not within the province of this paper to discuss the relative significance of these matters, the evidence is so overwhelming that the theory is generally accepted. It is also no doubt true that some groups of Echinoderms took to a free-living existence early in their ancestral history, and others remained fixed until comparatively a late period. As proof we may cite the embryological evidence that Holothurians develop without any attached stage whatever. that the Asteroids develop a larval organ and pass through a Sessile stage for a brief period in their development, while the crinoids usually remain permanently fixed throughout life. At least we can best account on this theory for the deep-seated and fundamental radial symmetry of some forms; the longer the attachment the more deep-seated would become the type of radial symmetry. Now if this theory is correct we can use it to explain the conditions described above for Thyone. The ancestors of this form must have broken away from the fixed stage very early, for we find the radial symmetry not well established on the right side of the animal as evidenced by both the position and size of the Polian vesicles. Out of 118 large and medium-sized Polian vesicles, 112 were on the left side, while in a total of 28 small or rudimentary Polian bodies, 25 were found on the right side. The arrangement of these organs in Thyone adds one more bit of evidence to support the following statement of Lankester.

It therefore appears that the Holothurian stock branched off from the Pelmatozoa before complete pentamerous symmetry of the hydrocoele and associated organs had arisen, before any definite calcynal system had developed, while the gonads were still a simple strand opening to the exterior by a single posterior gonopore.

The muscles used as retractors of the œsophagus were other organs in which there was considerable individual variation. As a general rule each of the five retractor muscles consists of a single band that takes its origin from the longitudinal radial muscle about one third the way back from the anterior end of the body and is inserted in front into the wall of the esophageal ring. Such a retractor, however, is frequently split up into several strands varying from two to five in number. A reference to Table III

TABLE III

To Show the Correlation between the Number of Polian Vesicles and the Tendency for the Retractor Muscles to Divide

Number of Polian Vesicles	1	2	3	4
Retractor muscles, single	39	2	0	0
Retractor muscles, multiple	1	17	15	2
Average number retractor muscles, per individual	5.153	10.263	12.400	10.000
Average number retractor muscles, per radius	1.030	2.052	2.480	2.000

shows that in 76 individuals examined, 41 had retractor muscles all in single bands, while 35 specimens had these muscles subdivided or multiple in character. This variation is especially interesting when considered with reference to the number of Polian vesicles. For in forty cases where one Polian body was present thirty-nine bore the unsplit or single retractor and there was only one specimen with these muscles showing a multiple number. In thirty-six cases where two or more Polian vesicles were present, all but two had the retractor muscles in a split or divided condition. If we consider each strand as a separate retractor muscle, we may then obtain the average number of retractors per individual for any definite number of Polian vesicles. By a reference to the fourth horizontal line of Table III, one finds that the average number in individuals with one Polian vesicle is

just slightly in excess of five, the pentameric number, and the average number when two Polian vesicles are present is 10.263. This ratio is only partly maintained when three vesicles are present, for the average number is then 12.400, and in the two cases with four vesicles the average was just twice the pentameric number. It is therefore evident from the facts shown in this table that with an increase in the number of Polian vesicles there is associated a strong tendency for the retractor muscles to take on a split character. If it were not for the fact that the split character shows considerable variation in the same individual one might suggest that the tendency to divide is correlated with the greater functional activity of the water vascular system as evidenced by the increased number of Polian vesicles and the location of the longitudinal muscles that lie along and just internal to the radial canals. About all one can say is that correlated with a more complete radial symmetry with respect to the Polian vesicles, there is a greater plasticity in the retractor muscles, causing them to divide longitudinally into separate muscle bands.

To what extent, or how completely, may these individual variations be reproduced in the process of regeneration? An answer was obtained in the following way. First a close examination was made of all parts eviscerated and a record was kept of all organs showing variable structures. Special attention was given to Polian vesicles and to retracter muscles. The mutilated specimens were then placed in separate aquaria in which the water was changed frequently to prevent it from becoming stale. After a considerable interval these animals were killed and the regenerated organs were compared with the lost parts. Table IV shows several individuals compared in this way. The number of retractor muscles found in each radius is given in the order of the radii taken in a clockwise direction. A study of the table indicates that there is a strong tetndency to reproduce individual peculiarities, as shown by individuals *B, E, G, H, M* and *O*. This does

not always hold true, for individual *L* reverted toward the more radial type of symmetry. From these few cases it would appear that individual peculiarities tend to predominate over ancestral influences in the process of re-

TABLE IV

To Illustrate the Relation between Regeneration and Original Symmetry in Thyone

Individual Used	Original Symmetry		Regenerated Symmetry	
	Polian Vesicles	Retractor Muscles	Polian Vesicles	Retractor Muscles
B	2	2–2–2–2–2	2	3–3–2–3–3
E	2+	3–3–2–2–2	2	2–3–2–2–2
G	2	1–1–1–1–1	2	2–1–1–1–1
H	2	1–2–2–2–1	2+	2–2–2–2–2
L	1	1–1–1–1–1	2	2–3–2–2–2
M	1	1–1–1–1–1	?	1–2–1–1–2
O	3+	2–2–2–2–2	?	2–2–1–2–2
W	..	....	2	2–2–2–3–4
X	..	....	2	2–2–2–2–2
Y	..	....	2	2–2–1–2–2

generation. Specimens *W, X, Y,* are included in this table to show further the correlation between Polian vesicles and retractor muscles.

Discussion and Summary

There remains to be discussed the general bearing of the foregoing experiments. First, the difference in the number of Polian vesicles in different Thyone is partly compensated by a variation in size, the fewer the number the larger their size, though this ratio would not be an exact one. In other words the total volume of the Polian vesicles in any given specimen bears a general relation to the size and functional activity of the animal. Notwithstanding this functional relationship since the actual number varies so widely it would be interesting to compare the number found in other species of holothuria with the conditions in Thyone. The data secured on this question were meager and not very definite. For example, Packard in one of the older text-books says in speaking of Thyone,

There are three Polian vesicles, one fusiform and an inch in length, the two others slenderer.

Clark ('02) gives the number for *Thyone briareus* (Leseur) as usually one or two; for *T. scabra* (Verrill) as usually single, and for *T. unisemita* (Stimpson) as one. He also mentions six other holothurians found in the Woods Hole region and all have a single Polian vesicle except *Cucumaria frondosa* (Gunnerus), which usually has one. He says nothing of the position in which these vesicles are found. In another paper ('01) Clark mentions a large holothurian about 40–45 centimeters in length (*Holothuria mexicana* Ludwig) in which there is a great diversity in the number of tentacles and Polian vesicles. The tentacles vary from 18 to 21, while the Polian vesicles vary from 1 to 9. The number of specimens examined, sixteen, was hardly sufficient to obtain an adequate comparison; two had 1 vesicle each, two had 2, five had 3, three had 7, one had 8, and one had 9. It is probable that if one were to examine a large number of individuals of each species, with reference to the number and location of the vesicles, he would obtain further interesting results. Lang ('96) cites a number of groups of holothurians in which only one vesicle has been observed; but states that there are a number of species in other groups that have occasionally or usually more than one.

Where accessory vesicles occur they vary greatly in number, and appear to have very slight, if any, systematic significance. Where only one Polian vesicle occurs it lies in the left ventral interradius, very seldom in the left dorsal interradius. Where two or more vesicles occur, they are also mostly formed in the ventral region of the circular canal.

Since Lang describes Cucumaria as the type specimen, in which the Polian vesicle is said to be in the left ventral region, it is possible that his generalizations were based principally on this form. At any rate, the conditions in Thyone seem to give a more definite significance to the number and location of the Polian vesicles.

Various explanations of autotomy and evisceration have been suggested, many of them having a teleological character. The view that the holothurian offers up the better

part of itself to appease the hunger of its enemy lacks confirmation, since the viscera are distasteful to fishes and to some other animals. It may be that the autotomous elimination of the Cuvierian organs serves a defensive purpose, as pointed out by Ludwig and Minchin, and Minchin suggests that the viscera may also be lost in this process and thus incidentally be associated with a protective response. In the case of Thyone, however, evisceration can hardly be considered defensive, and certainly it is not a process of self-division for only one part produces a new individual. Clark ('99) in discussing self-mutilation in the synaptas states the matter clearly in the following terms:

> I agree entirely with Cuenot ('91) in believing that autotomy is not normal or defensive but is due entirely to pathological conditions. I never saw a case of it in synaptas supplied with plenty of sand and an abundance of sea water.

Lang ('96) points out one of these pathological conditions, and recounts the fact that

> A Stichopus was observed to come entirely out of its skin, *i. e.,* the whole integument dissolved into slime, so that only the dermo-muscular tube enclosing the viscera remained.

In the present paper I have mentioned that Thyone at times appears to undergo a similar softening of the tissues in the region where the break occurs, and Pearse ('09) showed that autotomy is due, at least in part, to a structural arrangement which he considers is accidental in character. My observations further show that local constrictions undoubtedly have an important part in separating the retractors from the radial longitudinal muscles. All of these factors are pathological and are due to external or internal stimuli. The external (extra-cellular) stimuli, mechanical and chemical, as tried by Pearse ('08), appear to be less effective in producing autotomy than the purely internal (intracellular) stimuli such as lack of oxygen and its associated phenomena. The chemical (strychnine) that produced the largest percentage of evisceration in Pearse's experiments, probably affected respiration, since it greatly increased the activity of the

animal; therefore the need of oxygen would be proportionately greater than the supply, and the Thyone rendered more susceptible to evisceration. Now while autotomy undoubtedly enables the animal to maintain its existence for a considerable period on a smaller supply of oxygen, the times when this would become necessary in nature are probably rare, and it would be futile to speculate upon what evolution yet has in store for the process.

According to Lang, the retractor muscles of the oral region have been derived by the splitting up of the originally simple longitudinal muscles, and this specialization became more marked as the oral tentacles became more highly developed and required increasing protection. Species are to be found in the Dendrochirotæ in which the separation and branching off of retractors from the longitudinal muscles has not yet been perfected. In regeneration the retractor muscles of Thyone are derived in the same way, *i. e.*, by splitting off from the longitudinal muscles, and such progress is made that they are fairly well developed by the time the tentacles take up the function of feeding. The increasing sensitiveness and the later activity of the regenerating animal are presumably associated with the development of a new nervous system.

If we may regard the bilateral echinoderm larva as representing an early phylogenetic stage rather than a larval adaptation to a free-swimming existence, we will now discuss the symmetry of Thyone. As stated above, it is generally agreed that the radial arrangement of parts of the echinoderm body is due to a fixed stage in its ancestral history. Some holothurians and spantangoids, show in their ontogeny first a free stage, second a radial stage, and finally a bilateral adult. During the development of asteroids that have a fixed embryonic stage, the early bilateral symmetry is soon disarranged by the development of organs on the left side of the animal. For example, the left hydrocœle takes the form of an unclosed water-vascular rosette which grows around the esophagus to form the ring canal and its appendages, and its connection with the dorsal pore gives rise to the stone

canal. Excepting the echinoids and crinoids in which there is either no distinct Polian vesicle or else a simple glandular structure, those echinoderms that have retained the most distinctive type of radial structures have also as a rule, retained the most symmetrical arrangement of the Polian vesicles. Presumably these forms, the asteroids and ophiuroids, have quite recently abandoned the fixed stage, and each individual usually has four Polian vesicles and a stone canal, one in each interradius. Among most of the holothurians a secondary bilateral symmetry has become superimposed over the radial type, and it is reasonable to suppose that there was a time in the ancestral history of Thyone when the Polian vesicles were symmetrically and radially disposed, or else the animal quit its fixed habits before the radial symmetry of the vesicles was thoroughly established. In the one case we would have a regression, a sort of backward retracing of the steps of evolution, or, which seems more probable, the ancestors of Thyone began a free-living existence before the radial arrangement of the Polian vesicles had become complete. Also the fact that the embryology of the holothurian egg is probably much compressed and shows no trace of a fixed stage indicates that the corresponding ancestral stage was comparatively short, or, very remote. Since the modern habits of Thyone are bilateral, and since it is altogether improbable that such habits would produce the present arrangement of Polian vesicles, the position of these organs must be due to ancestral influence.

Now the Polian vesicles are capable of contracting and expanding and their function when they are well developed is to act as accessory reservoirs of the water-vascular fluid. Muscle and connective tissue in the wall of the vesicle furnish the means to do this work. Of course, if the ampullæ are well developed there is little or no need of Polian vesicles, as is the case in Asterias. But, though the size and number of these vesicles is functionally correlated with the general development of the water-vascular system, especially of the oral tentacles,

and hence shows great variability in the different species of holothurians, this does not in any way explain the great excess of these vesicles on the left side of *Thyone briareus*. In regeneration, probably through the influence of functional correlation, there is a tendency for the old tissue to reproduce the exact number and arrangement of the lost vesicles, but it may reproduce a somewhat more radial (ancestral) arrangement.

Enough has been given in this paper to show the need of a more extensive and intensive reexamination of the Polian vesicles. This would give a better idea of their morphological and functional significance. The following summary and conclusions are based on the work described:

1. Evisceration in Thyone includes the following organs: Esophagus, stomach, intestine, calcareous ring, nerve ring, tentacles, ring canal, Polian vesicles, stone canal with madreporite, and the retractor muscles of the esophagus.

2. The method used to produce evisceration was to allow Thyone to stand in stagnant water until it became foul. This was followed by treatment with running water containing much oxygen. Alternating these processes produced as high as 65 per cent. of self-mutilated individuals.

3. The structural accident theory of Pearse is inadequate to explain all of the conditions arising in the process of autotomy. At times the skin appears to dissolve away with little or no pressure present, and retractors frequently break off by local constrictions instead of by longitudinal pull.

4. The parts eviscerated are at first highly irritable, and may be kept alive for some time. The part remaining is less responsive, but reacts to touch, to lack of oxygen, and probably to other stimuli.

5. Regeneration of all lost organs may occur, but it takes place only when all parts concerned in evisceration are completely expelled. Otherwise the animal dies.

6. During the process of regeneration the behavior gradually becomes more responsive and finally is like the normal individual. This appears to be correlated with the growth of a new nervous system.

7. Thyone is functionally a bilateral animal, but the most conspicuous individual differences involve structures that have a radial arrangement.

8. The Polian vesicles vary greatly in number, size and location. There is a strong tendency for these to occur on the left side, and this arrangement is undoubtedly due to ancestral conditions, for the present bilateral habits of Thyone could probably have no influence in producing this asymmetry.

9. The retractor muscles in a single radius consist of single or multiple strands, and this variation is closely correlated with a similar variation in the number of Polian vesicles. No explanation is forthcoming for this peculiar plasticity of the retractor muscles, but the suggestion is made that it may be functionally correlated with the development of the water-vascular system.

10. It was found from the study of a number of specimens that individual peculiarities of structure tend to be reproduced in the process of regeneration. In this process it would appear that individual variations tend to predominate over generalized ancestral influence.

11. Autotomy enables Thyone to survive for a considerable period on a smaller than normal supply of oxygen. Nevertheless, the conditions which give rise to self-mutilation are seemingly in all cases pathological.

12. The conditions in Thyone afford some evidence for believing that when this animal abandoned the fixed stage the Polian vesicles conformed more or less to the radial type. This is opposed to the statement of Lang that in all cases where a multiple number is now present "there was originally only one vesicle." It is believed that the present arrangement of Polian vesicles in Thyone can be best accounted for on the theory of phylogenetic influence. That, in general, those vesicles have retained their most complete radial arrangement in those species of

echinoderms which have maintained to a high degree the functional activity of the water-vascular system.

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SHORTER ARTICLES AND DISCUSSION

TERMS RELATING TO GENERIC TYPES

In the field of biological taxonomy an important reform is in progress. The change is from the method of concepts to the method of types, in order that names may be applied with greater precision and permanence. Under the method of types we no longer think of the technical name of a plant or an animal as attaching primarily to a concept embodied in a description or definition, but as relating to the first representative of the group that became known to science. In determining the application of a specific name we go back to the original specimen or type on which the description was based. The original description has become secondary to the original specimen. In like manner generic names are treated as relating primarily to groups of species, with the original species as the generic type.[1]

Without waiting to appreciate the fundamental nature of the change from concepts to types, many systematic workers took it for granted that generic types were to be determined by elimination, in much the same way that generic concepts had been treated, by gradual subdivision, restriction and removal of component groups. The general results of elimination were the same as under the method of concepts. The applications of many of the older generic names did not become definitely fixed, but remained dependent upon varying individual opinions of the validity of the work of later authors. It often happened that after elimination was accomplished only the doubtful or unidentifiable species remained to serve as generic types. Gradually it became apparent that the practise of elimination was inconsistent with the method of types, and could not insure stability in the application of names. Recourse was then had, especially by zoologists, to the arbitrary designation of generic

[1] Cook, O. F., 1898, "The Method of Types," *Science*, N. S., 8: 513; also 1900, "The Method of Types in Botanical Nomenclature," *Science*, N. S., 12: 475, and 1902, "Types and Synonyms," *Science*, N. S., 15: 646. Swingle, Walter T., 1913, "Types of Species in Botanical Taxonomy," *Science*, N. S., 37: 864.

types, the apparent object being to preserve the results of elimination, even though the theory had to be abandoned. Probably it is only a question of time until the results of elimination will be discarded, as well as the theory, and replaced by the actual, historical types.

A plan for determining the historical types of genera was adopted in 1907 in the American Code of Botanical Nomenclature, and other applications of the method of types are being rocognized by zoologists. Specialists in many groups are engaged in the study of generic types, and the need of a special terminology to facilitate work of this kind is becoming apparent. Thus in Bulletin 83 of the U. S. National Museum, "Type Species of the Genera of Ichneumon Flies," by Henry L. Viereck, two new terms, "isogenotypic" and "monobasic," are employed in treating of the application of generic names to type species. The paper is of interest, not only to students of this group of insects, but also as an example of the tasks that confront all taxonomists who appreciate the need of basing their work upon types. The distinctions to which the special terms refer are undoubtedly useful, and the possibilities of expressing them in more convenient form are worthy of consideration.

The word "isogenotypic," is used with reference to cases where two or more generic names have been applied to the same type species.[2] For this purpose a new term is not needed unless zoologists are unwilling to borrow from botanical nomenclature a more convenient method of treating the same class of cases. The botanical code provides a classification of synonyms, and applies the word "typonym" to a name that has to be rejected because an earlier valid name was proposed for the same type. The formation and use of typonym are in accord with a familiar analogy. As a preoccupied name becomes a homonym, it is easy to remember that the use of a preoccupied type results in a

[2] A different combination might have been expected, such as "autogenotypic" or "deuterogenotypic," since isogenotypic suggests the notion of equally good types or of equal numbers of types, instead of conveying the idea of one and the same type, or of a second use of the same type. Genera have been termed "isotypical" when they were described from more than one species, but all truly congeneric, on the assumption that such species would have equal standing as types. A still older use of the word "isotype" had reference to equal representation of a genus by similar or corresponding species in different geographical regions or geologic periods. See Schuchert, Charles, 1905, U. S. National Museum Bulletin 53, Pt. 1: 16.

typonym. A name based on a different type species, but congeneric with the type of an older genus, is termed a metonym. A name rejected for lack of an identified type is a hyponym, and one rejected for linguistic reasons, a caconym. All rejected names fall readily into these five classes.

The other new term, "monobasic," is used by Mr. Viereck to indicate genera with only one species at the original place of publication. In botanical literature the word "monotypic" is often employed in this sense, though also applied to genera that consist of only one species. If previous use disqualifies monotypic, the same objection lies against monobasic. In addition to an older chemical meaning, the same word was employed several years ago in a biological sense, to describe a condition of descent in simple lines.[3] Apart from being preoccupied, the word monobasic has a misleading implication, since under the method of types each generic name is referred to a single type species. The idea of a genus being based on many types is discarded with the method of concepts. Appreciation of this incongruity may explain why no such term as "symbasic" or "polybasic" is used in contrast with monobasic, to indicate genera that were first proposed in connection with more than one species.

Evidently there is need of a simple and consistent terminology for indicating relations between generic names and type species. The normal relation under the method of types is the designation of the type species at the original place of publication of the genus. Genera provided with types by original designation may be described as *orthotypic*, or normal-typed. With orthotypic genera there is no occasion to raise the question of how many species were included at the original place of publication.

[3] Cook, O. F., and Swingle, W. T., 1905, "Evolution of Cellular Structures," Bull. 81, Bureau of Plant Industry, U. S. Department of Agriculture, p. 20. Plants or animals with specialized habits of asexual reproduction, such as vegetative propagation, parthenogenesis or self-fertilization, would be described as monobasic. The second edition of the Standard Dictionary defines monobasis as follows: "The derivation of a stock from a single parentage by inbreeding, or by propagation of buds or cuttings; opposed to symbasis." Thus the danger of ambiguity in using monobasis for nomenclatorial purposes is greater than in using monotypic, though it must be admitted that the use of the word monotypic in two senses may sometimes result in confusion. Genera that were monotypic in the strictly nomenclatorial sense of being established in connection with one species may not be monotypic in the more general taxonomic sense of including only one species.

Genera that are not orthotypic fall into the two classes already considered, those with a single species at the original place of publication, and those with two or more species. It is now generally agreed that when only one species was mentioned this should be accepted as the type. Such genera may be called *haplotypic*, or single-typed. When two or more species were included in the original treatment of a genus, and no type was designated, we have the problem of subsequent determination of the type, resulting in what may be termed a *logotypic* genus, that is, a genus with a rationally selected type species. The object of selection is to determine the historical type of the genus. Names must have definite applications, and historical applications of generic names can be made definite by ascertaining the historical types. The recognition of a new generic group is usually based on one leading or dominant species, with the others added as associate members.

In many cases the generic type is intimated by the original author in dividing the genus into subgenera or sections, in illustrating one of the species or citing illustrations published in earlier works, in naming the genus with particular reference to one of the species, in recording economic uses, or in giving geographical or other indications of greater familiarity with one of the species. If the application of these or other historical criteria leaves more than one species eligible for selection, the first of the eligible species should be taken as logotype. In this way it is possible to develop a consistent system of type selection that will commend itself as reasonable and give the same results in the hands of different students.[4]

[4] Simply taking the first species under a generic name as the type would probably establish more of the generic names in their historical places than the method of elimination, which accepts the last of the original species left in the genus as the type. Either of these methods of selecting types would result in many cases of separation of generic names from their historical types, but these undesirable changes in the application of names can be avoided by taking the historical considerations more directly into account, as in the American Code of Botanical Nomenclature. Probably a more satisfactory system for associating generic names with their historical types could be developed by sufficient study of the problem. A policy of refusing to revive generic names that were not directly associated with binomial species to serve as types, would avoid many of the changes threatened by unmitigated priority. In proposing lists of "*nomina utique conservanda*" in advance of any provision for the definite application of names, European botanists have demonstrated one more way to put the cart before the horse.

In addition to the three ways of associating generic names with their type species, there are many cases where generic names have been applied to groups that do not include the type, or any of the original species. Formal assignments of erroneous types also occur when generic names are not traced back to their original places of publication, or when ineligible species are designated as types. In dealing with the synonymy of genera previously treated under names that belong to other groups it will be convenient to have a distinctive term for this class of cases. Such misplaced names, applied to groups that do not contain the true type, may be indicated as *pseudotypic*, or false-typed.[5]

It should be expected that more critical analysis of taxonomic problems would lead to more definite distinctions and more precise terms. The older terminology was developed to facilitate the study of names, whereas it is now apparent that provision must be made for the study of types as another formal branch of biological taxonomy. Nomenclature has a history of three hundred years while systematic typology is only beginning. To gain further insight into these typological problems is obviously more important than to attempt premature applications of partial solutions. It may take fifty or a hundred years to transfer

Failure to regulate the application of names is the fundamental defect of the Paris and Vienna codes, and is hardly to be cured without thorough recasting.

[5] Thus the palm genus *Martinezia*, as treated by Kunth, Martius, and many later writers as relating to *Martinezia caryotæfolia* and its immediate relatives, was pseudotypic, for this species does not appear to be congeneric with any of the five species originally referred to *Martinezia* by Ruiz and Pavon. Hence it has been proposed to replace this pseudotypic use of *Martinezia* by a new generic name, *Tilmia*. (See *Bull. Torrey Bot. Club*, 28: 565.) The five original species of *Martinezia* belong to three natural groups, now recognized as distinct families, the first two species to the Cocaceæ, the third species to the Acristaceæ and the others to the Chamædoreaceæ. The third species, *M. ensiformis*, should be taken as logotype of *Martinezia* because the figures used to illustrate the generic characters evidently represent a member of the family Acristaceæ. Another reason for excluding the cocoid species from consideration as type is that they are mentioned as deviating from the "essential characters of the genus," in connection with the original description. The rule of the Vienna code, to the effect that the name of a subdivided genus should go with the majority of the species, would carry the name *Martinezia* over to the family Chamædoreaceæ. The making of such a rule shows that many European botanists were still working under the method of concepts, and were not accustomed to think of generic names as inseparably connected with type species.

the whole structure of biological taxonomy to the new foundation of types. To suppose that any permanent advantage can be gained by elaborating defective methods under forms of legislative enactments or judicial decisions is to show a limited appreciation of the nature of the subject and of its historical development. As long as legislation and interpretation are based on inadequate study, they can represent, at most, only a temporary consensus of opinion, for it is of the very nature of science to condemn and throw aside any doctrine or method that has proven inadequate or fallacious.

Terms Relating to Synonyms

The following classes of synonyms were recognized in 1907, in the American Code of Botanical Nomenclature:[6]

Homonym.—A name rejected because of an earlier application of the same name to another genus.

Typonym.—A name rejected because an older name was based on the same type.

Metonym.—A name rejected because an older valid name was based on another species of the same genus.

Hyponym.—A name not associated with a type.[7]

[6] *Bulletin of the Torrey Botanical Club*, 34: 167, 1907.

[7] Much confusion would be avoided by a consistent policy of withholding recognition of generic names that have not been associated with type species. Thus the name *Acoeloraphe*, proposed by Wendland in 1879 in an analytical key to genera of fan-palms (*Bot. Zeitung*, 37: 147), was not associated with a type, though evidently relating to a species mentioned in the same paper as ''*Brahea serrulata.*'' This Florida palm differs from the Mexican type of *Brahea* in the leaf characters assigned to *Acoeloraphe* in the key and in the seed character indicated by the generic name, the albumen being solid instead of having a deep channel along the raphe. But *Acoeloraphe* being left without a type, another name, *Serenoa*, was proposed by Hooker f. in 1883 for ''*Sabal serrulata* R. & S.'' (Genera Plantarum, 3: 926). All subsequent writers have accepted Hooker's name, and *Acoeloraphe* should remain under *Serenoa* as a hyponym. Nothing has tended so strongly to bring the principle of priority into disrepute as the incontinent revival of abortive names, to replace properly established names in current use. No species was referred to *Acoeloraphe* until 1907, when Beccari (Webbia, 2: 107) applied the name *Acoeloraphe wrightii* to a Cuban member of a genus that had been described in 1902 under the name *Paurotis*, a Bahaman species, *Paurotis androsana*, being the type (*Mem. Torrey Bot. Club*, 12: 21). This transfer of the name *Acoeloraphae* to the genus *Paurotis* was followed by Sargent in 1911 (Trees and Shrubs, 2: 117), but Beccari's genus *Acoeloraphe* is a metonym of Paurotis, and is also pseudo-

Terms Relating to Type Species

Orthotype.—Type by original designation. A species designated as type in connection with an original publication of a generic name. A genus whose type was formally designated at the original place of publication is orthotypic.

Haplotype.—Type by single reference. A single species referred to a genus at the original place of publication, and on this account accepted as the type. A genus proposed with reference to a single species is haplotypic.

Logotype.—Type by subsequent determination. The historical type of a genus, selected from two or more original species. A genus whose type is selected from two or more original species is logotypic.

Pseudotype.—Erroneous indication of type. A species erroneously indicated as the type of a genus. A genus treated on the basis of an erroneous type, or so as to exclude the true type, is pseudotypic.

O. F. Cook

Bureau of Plant Industry,
U. S. Department of Agriculture,
March 13, 1914

typic, because of the original application of the name to *Serenoa.* Two species of *Paurotis* are supposed to exist in Florida, one that is identified with the Cuban *P. wrightii* (Grisebach & Wendland) and a local species, *P. arborescens* (Sargent).

NOTES AND LITERATURE

LINKAGE IN THE SILKWORM MOTH

One of the most striking recent developments in the study of genetics is the discovery of linkage in many of those forms which were supposedly thoroughly worked out. The most recent example is a very interesting paper by Y. Tanaka,[1] entitled "Gametic Coupling and Repulsion in Silkworms." The data presented in this paper demonstrate the existence in the silkworm moth of a group of four pairs of linked genes. Following Tanaka's nomenclature we may designate these genes as follows: *N*, which differentiates the larval color pattern known as "normal" from that called "plain"; *S*, occurring in larvæ having the "striped" pattern, and epistatic to *N*; *M*, the differentiator for the "moricaud" larval pattern, also epistatic to *N*; *Y*, the gene which differentiates caterpillars with yellow blood and yellow cocoons from the recessive whites. Of the six possible combinations of these genes, taken two at a time, all but *NM* and *SM* were made, and all showed linkage. F_2 "coupling" tests, *i. e.*, from matings where both dominants entered the cross from the same P_1 individual, were made for *SY* and for *MY*. In each case there occurred cross-overs, or new combinations of the characters, in such proportions as to lead Tanaka to suppose the ratio of parental combinations to cross-overs among the gametes to be about as 7:1. "Repulsion" (where one dominant entered from each P_1 individual) F_2 results were obtained for *NS* and for *NY*. In neither case did any double recessives (cross-overs) appear, though over 3,000 caterpillars were obtained in the case of *NY*, and 224 in the case of *NS*. From these data Tanaka concludes that the repulsion was complete in these two cases. It has, however, been pointed out by Morgan[2] that such results will be obtained if the linkage is complete in one sex only. In *Drosophila* such "repulsion" crosses never produce double recessives in F_2, and it has been shown that this is due to complete linkage in the male, crossing over being frequent in the female between some pairs of genes. In order to test this possibility it is necessary to mate doubly heterozygous individuals to double recessives, when the gametic ratio is obtained directly and without the complications present in most F_2 results. It so happens that Tanaka reports two such crosses, one for each sex, though he does not recognize their im-

[1] *Jour. Coll. Agr.*, Tohoku Imper. Univ., Sapporo, Japan, V, 1913.

[2] *Science*, N. S., XXXVI, 1912.

portance in this connection. When a male heterozygous for S and for Y, one dominant having been derived from each parent ($SysY$), was mated to a doubly recessive ($sysy$) female, there were produced 63 Sy and 65 sY—no cross-overs. A female heterozygous also for S and for Y, but having them "coupled" ($SYsy$), was mated to a male $sysy$, and produced 215 SY and 188 sy—again no cross-overs. Yet that crossing over may occur between these two pairs of genes is shown by the fact that the "coupling" F_2 results indicated a gametic ratio of about 7 : 1 : 1 : 7. We are, therefore, still left in the dark as to whether crossing over occurs in only one sex, or in both. But it is certain that the strength of linkage in this case is not always the same—a point of great interest and importance. Similar cases have been reported by Baur[3] in *Antirrhinum*, by Punnett[4] in the sweet pea, and by the writer[5] in *Drosophila*.

Tanaka refers to his case as differing from previously reported cases of linkage in animals in that the sex differentiator is not one of the genes involved, and in that the linkage is sometimes only partial. However, he refers several times to a paper by Morgan[6] in which it is clearly shown that three of the sex-linked genes in *Drosophila* also show partial linkage to each other, independently of their sex-linkage. Punnett,[7] in referring to the same paper, has said, "Morgan's experiments with *Drosophila* suggest coupling of some kind between factors for eye color and shape of wing, though both of these factors may show sex-limited inheritance in other families." A study of the data referred to, or of any of the similar data on *Drosophila* since published, will show that these genes *always* show sex-linkage, and that *at the same time* they always show linkage to each other when both can be followed in the analysis. The two phenomena are not mutually exclusive, but both are always present.

Both Tanaka (in a footnote) and Punnett refer to the latter's case in rabbits as the first example of linkage in animals not involving sex. If the linkage between sex-linked genes is, for some strange reason, not considered to belong in this category, there are still at least two cases which antedate Punnett's slightly. A few months before Punnett's paper appeared I had suggested[8] the possibility of linkage in mice. It now seems rather probable that the relation in both mice and rabbits may really be that of

[3] *Zeits. f. ind. Abst.-u. Vererb.-Lehre.*, VI, 1912.

[4] *Jour. Genet.*, III, 1913.

[5] *Science*, N. S., XXXVII, 1913.

[6] *Jour. Exp. Zool.*, XI, 1911.

[7] *Jour. Genet.*, II, 1912 (Nov.).

[8] AMER. NAT., XLVI, 1912 (June).

triple allelomorphism. For this reason I am inclined to assign priority to Morgan and Lynch,[9] whose paper on linkage of genes in *Drosophila* which are not sex-linked appeared after my own paper and before Punnett's.

COLUMBIA UNIVERSITY A. H. STURTEVANT

NABOURS'S BREEDING EXPERIMENTS WITH GRASSHOPPERS

IN a recent paper, Nabours ('14) describes breeding experiments that he has been carrying on for some years with grouse locusts of the genus *Paratettix.* His work is of special interest in showing that in a wild species there exists a number of distinct types that show alternative inheritance of a particular kind. His paper may be summarized as follows:

1. Nine distinct, true breeding forms of *Paratettix* were collected "in nature." These "species" (as Nabours is inclined to consider them) "are mainly distinguished by their striking color patterns."

2. When an individual of one of these species is mated to one of a different species the hybrid character of the offspring is apparent at once, in that "all the characters of each parent are represented in the F_1 hybrid." In other words, the hybrid is in a certain sense an intermediate, and "the terms dominant and recessive" are probably not "applicable at all." This point, while of little theoretic importance, has a practical value in that the zygotic constitution of any hybrid can be recognized without further breeding tests.

3. With one exception, each color pattern factor was found to behave as an allelomorph to any other color pattern factor.

4. The various lengths of the wings and pronotum are apparently not inherited, as such but are determined by environmental factors, especially such as tend to prolong or to shorten the length of larval life.

It appears that Nabours confuses the relation of the facts mentioned under 3, and that he supposes this to be the ordinary behavior of "mendelizing characters," for he says:

> The essential result of these experiments has been the extension of this principle [Mendelian inheritance] to a considerable number of types of a phylogenetically low group of ametabolous insects.

To be sure, he recognizes that other workers in genetics have an attitude quite different from his, and he takes some little pains to make clear his own point of view. To quote again (p. 142):

[9] *Biol. Bull.*, XXIII, 1912 (Aug.).

The existence of unit characters in the De Vriesian sense does not appear to have been as clearly demonstrated as that of alternative inheritance . . . and the interpretations are at great variance. Thus, one group of authors [reference made to Bateson, Doncaster, and Tower] recognize characters in organisms that can be replaced by other characters when the proper crosses are made, . . . while on the other side there are those [references to Whitman and Montgomery] who believe that the organism as a whole is the only unit and that there are no actual unit characters.

Again he says (p. 169):

No character of one parent species is ever replaced in the F_1 hybrid by any character of the other parent. All the characters of each parent are represented in the F_1 hybrid. It follows then that these grasshoppers do not exhibit characters which by crossing can be replaced by other different characters; the whole pattern appears to be the only unit.

There is no real conflict between Whitman's idea and the accounts given by students of Mendelism, for the latter realize that far-reaching somatic effects may result from a single factor, and the composite character of the hybrid is not an uncommon occurrence. Nabours identifies a particular pattern with the "organism as a whole," but since his evidence relates here to color patterns only, nothing is gained by the introduction of such a vague phrase as the "organism as a whole." Specifically he shows that the hereditary differences between any two types can be explained on the assumption of a single differential for each case.

With reference to the antithesis presented by Nabours, it must be recognized that the modern literature of Mendelian heredity affords innumerable instances where two or more characters entering from one parent and their allelomorphs from the other, reappear in the F_2 generation in new combinations.

If we assume with Nabours that each of the eight color patterns are represented by a characteristic condition of the "germinal material," we may use his terms *A*, *B*, *C*, *D*, *E*, *F*, *H* or *I* to symbolize this "germinal material" for the various color patterns. As Nabours uses the terms, an individual homozygous for *A* is represented simply by *A*, and a hybrid between *A* and *B* by *AB*. In ordinary usage, the homozygous form would be represented as *AA* and its germ cells by *A*. This is a minor matter. Ordinary usage has the advantage of being more consistent.

According to Nabours, then, *A* mated to *B* gives *AB*; *B* mated to *F* gives *BF*; *C* mated to *E* gives *CE*, etc. In gametogenesis these factors segregate, so that, for example, *BA* gives germ cells

A and *B; BF* gives *B* and *F,* etc. In other words, he treats the matter as if he were dealing with a system of multiple allelomorphs, though he nowhere specifically calls them such. From this point of view there are eight distinct allelomorphs concerned with color pattern any two of which may constitute a pair; in any zygote two allelomorphs (perhaps alike, perhaps unlike) will be present, and in any gamete only one of the eight will normally occur.

With one exception of which I will treat later, all of Nabours's results can be explained by this hypothesis. This sort of explanation is not new. (Shull ('11), de Meijere ('10), Sturtevant ('13) and others have used it to explain results obtained in *Lychnis, Papilio,* rabbits and other forms, and it will almost undoubtedly be shown to apply satisfactorily in still other cases.

The exception just mentioned occurred in the cross which Nabours describes at the bottom of page 156 (*e*). Here a male of the constitution *CE* was mated to a female of the constitution *BI*. On Nabours's theory, the gametes of the male should carry *C* or *E*, but not both, and the gametes of the female should carry *B* or *I,* but not both. The union of the two kinds of sperms with the two kinds of eggs should give four classes of offspring, and these were in fact obtained; viz., 12 *BC,* 11 *BE,* 7 *CI,* 10 *EI*. But there appeared also one individual *BEI*. Nabours's explanation of the case is that perhaps the *BI* "female parent gave at least one gamete containing the factors for the patterns of both her parents and that this double character gamete was fertilized by one of the *E* gametes which came from the *CE* male."[1] Let us see whether this is the most probable interpretation.

As Sturtevant has pointed out, for any case to which the idea of multiple allelomorphism is applicable, an equally valid explanation may be found in "complete linkage" of the factors concerned. To decide in any case between the two explanations would be impossible.

If, however, linkage were not complete, a "cross-over" class or "recombination" class might occur, and this would suffice to rule out the explanation based on multiple allelomorphs.

Such a "cross-over" class perhaps is furnished by the *BEI* individual. The demonstration of this may be given by the use of symbols, as follows:

Let us assume that *A* is the allelomorph of *a*, *B* that of *b*, *C* of *c*, *D* of *d*, *F* of *f*, *I* of *i*, etc., making eight pairs of allelomorphs altogether. Assume that each gamete of any individual carries

[1] This explanation is essentially similar to that advanced by Bridges ('13) to explain certain peculiar results in *Drosophila*. Bridges assumed that in gametogenesis the two X-chromosomes of a white-eyed female failed to segregate (in Bridge's terminology, non-disjunction occurred), and passed over together into one gamete.

one allelomorph of each pair, and that the eight factors thus present in a gamete form a linked group, tending to segregate as a unit in gametogenesis. Thus Nabours's form *A* would give gametes of the form *Abcdefhi*. *AB* would give gametes of only two forms, one corresponding to *A* and the other to *B*, viz., *Abcdefhi* and *aBcdefhi*. Two other forms are possible, formed by the exchange of *A* with *B*, and of *a* with *b*, but these will not occur if linkage is complete. In dealing with the hybrid *AB* in practise the factors *cdefhi* would not be put into the formulæ, as they are alike in all gametes.

These rules would apply similarly to all other species and hybrids. Therefore in the case in which the *BEI* individual occurred, we would represent the male parent, which Nabours designated *CE*, by *bCei–bcEi*, and its gametes by *bCei* and *bcEi*. The female parent, which Nabours designates *BI*, we would represent by *Bcei–bceI*, and its gametes would be *Bcei* and *bceI* if linkage were complete. If linkage were not complete there would occasionally be formed gametes *bcei* and *BceI*. One of these latter (*BceI*) was probably formed and fertilized by a sperm of the type *bcEi*, thus giving rise to the *BEI* individual. No gametes corresponding to *bcei* appear to have been fertilized, though of course we do not yet know what the appearance would be of an individual so formed.

This matter would be easy to test, and it is to be hoped the cross may be repeated. If then *BEI* forms should appear again and in these when mated to other forms the factors B and I should be found to stay together to the same extent as they before separated, it would show that close linkage, rather than multiple allelomorphism explains this particular instance.

It may be, too, that both linkage and multiple allelomorphism play a part in the production of these phenomena. In any case it seems that the test is at hand, and not difficult to perform, excepting in so far as there are practical difficulties connected with the rearing of the grasshoppers in sufficient numbers to cover the point.

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SPECIES-BUILDING BY HYBRIDIZATION AND MUTATION

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THE mystery that has surrounded the origin of new species in the incipient stages of their evolution has lately been penetrated and cleared away to a large extent by the light of studies in Mendelian inheritance and the attendant idea of mutation. Species building is no longer a hypothetical process based on the preservation of minute, useful, fortuitous variations, but it is a process open to observation and experimental control. Its raw materials are variations that are usually not minute, useful or fortuitous, but clean-cut unit characters, tending to vary only in certain limited, well-defined directions depending upon the chemical peculiarities and physical structure of the particular form of protoplasm, and, in the vast plurality of cases, nonuseful.

The fields of systematic zoology and botany, illuminated by the new science, genetics, are emerging from the mists of formalism, and invite biologists of the broadest type to exploration. The geneticist turns to systematics for many of the materials with which to solve the problems of organic evolution. The systematist sees that in order to keep abreast of the times he must stand ready to rebuild his pigeonholes and test with experiment that which he puts into them.

Every one occupied with zoology or botany realizes that there are no adequate criteria by which this or that assemblage of individuals is or is not to be regarded as a

distinct species. Arbitrary rules for species making, designed to restrict the activities of the more vigorous "splitters" have been indeed laid down by experienced and conservative systematists. The final test, however, so far as any exists, is acknowledged to be whether a group breeds approximately true to its kind and is approximately sterile with other closely related stock, and yet in how few cases have both or either of these criteria been actually applied by the describer of species!

As a matter of fact no stock that has been bred on a vast scale, so far as I am aware, breeds absolutely true to specific characters. In Morgan's *Drosophila*[1] and De Vries's *Œnothera,* numerous mutants appear, probably through the absence of certain chemical elements, or by unusual combinations of elements, in the chromatin of the germ plasm. That this phenomenon has not been shown for many other species is due, in all probability, to lack of close attention to all the individuals in a huge procession of stock in the process of breeding. Any insect bred as extensively as *Drosophila ampelophila,* the pomace fly, has been would probably show as many mutants; some would show more. *Colias eurytheme,* the "orange sulphur" or alfalfa butterfly, is such an example. Though this butterfly can not be bred on a scale comparable with *Drosophila,* every thousand individuals yield many discontinuous variations: red eyes instead of green, tongue uncoiled instead of wound in close flat spiral when at rest, one antenna shorter than the other, the absence of certain spots from the wings, gynandromorphism, caterpillars with two longitudinal rows of large black dorso-lateral spots or white dorso-lateral stripes upon a dorsal surface usually unmarked, caterpillars with one proleg less upon one side than the other. This is a partial list of points at which the descendants of three females of *Colias eurytheme* failed in a single summer to breed true to the characteristics of the species, though bred under uniform normal conditions. The fact that these discontinuous

1 *Science,* N. S., Vol. XXXIII, Nos. 847, 849, pp. 496–499, 534–537, 1911.

variations appear under uniform external conditions leads one to be very skeptical toward most of the past experimental work supposed to show the effects of the environment upon insects in modifying the germ cells. Any one wishing to try an experiment on the production of variations by the influence of the environment, or upon the inheritance of acquired characteristics, should deny himself absolutely this privilege until he shall have bred under normal conditions at least a thousand individuals of the stock that he will subsequently employ.

That species necessarily breed true to the specific characters ascribed to them by their inventors is an unverified dogma. At best the reporter picks out stray individuals here and there from a vast procession of which he can only see glimpses, and, trusting to the credulity of the public in the established ideas about these matters, he creates upon paper a new species. Doubtless the unit characters of "specific" grade in the stock of some species are more generally constant or homozygous than those of certain others, but it is reasonable to suppose that, owing to dominance the heterozygous[2] condition regarding certain characters is frequently masked and unnoticed in apparently pure strains of wild stock. If the heterozygote respecting a certain character be comparatively rare, or if it be a heterozygote based on several interacting factors, like redness in the kernel of Nilsson-Ehle's wheat,[3] it may cross again and again with the homozygous dominant, or with another heterozygote of similar nature to itself, without the appearance in the population of the recessive. That specific and varietal characters do exist in heterozygous condition in wild stock of "pure" species, unmasked by dominance and easily detected, I have found to be the case in *Colias* at several points. The color pattern as a whole apparently fluctuates in variation, but these variations in detail are

[2] The mixed Mendelian condition, $D(R)$, producing germ cells D and R in equal numbers.

[3] *Act. Univers. Lund*, 1909.

strictly a matter of inheritance. Its "fluctuation" is not due to a difference in environmental conditions surrounding different individuals, but evidently to the condition of the germ plasm. The parents of any brood may be heterozygous or homozygous for the determiners of color pattern. If they come from a strain homozygous in this respect and are alike in appearance, the offspring will resemble the parents closely and show a narrow range of variation, but if unlike and derived each from unlike parents, a wide range of inherited "fluctuation" occurs. Such is often the case in the inheritance of a melanic tendency so often attributed to the action of the environment, and of spots used in the diagnosis of species as, for example, the conspicuous spot in the middle of the under side of the hind wing. This is commonly double in *Colias philodice* and *C. eurytheme,* consisting of a chief and an accessory spot, single in *C. palæno,* an arctic circumpolar species, but it varies enormously. In *eurytheme* and *philodice* the accessory spot may be absent; in *palæno,* in rare cases, it may be present. I have bred large families of *C. eurytheme* in which both the chief and accessory spots were, like those of the parents, almost uniformly large and nearly equal in size. In other families, from parents in which the accessory spot is nearly or quite lacking, the offspring show a similar reduction. In *C. philodice* I have found it possible by selection to establish a race devoid of the row of submarginal red-brown spots of the under side of the wings. Thus, by selection, strains, nearly or perhaps quite homozygous for definite points of color pattern, may be established, derived from a population which in the main is in an extremely heterozygous condition. Yet species are named and distinguished on the basis of these features.

Another example of heterozygous condition of a character within a wild species is the white pigment in the ground color of the "albino" female of *Colias,* both in the yellow species, *philodice* and the orange species, *eurytheme.* The white female is regularly heterozygous

for this sex-limited character. Her daughters are white or colored (yellow or orange, as the case may be) in equal numbers. Still another interesting heterozygous feature, though not of "specific" grade, was seen last summer in a pure strain of *Colias eurytheme.* A female appeared that could not upon stimulation coil up her tongue. Mated with a normal male, this abnormality was inherited in various degrees by half her offspring (37 uncoiled and 28 coiled). One of her daughters, abnormal in this respect and mated with a normal of a different strain, transmitted the abnormality to about 16 per cent. of her offspring (29:151), showing that the possessor of this abnormality is regularly heterozygous in respect to it.

Whether *Œnothera lamarckiana* is or is not a complex hybrid produced from two American species, is it not certain that, like other wild and cultivated stock, it does possess characters for which it is heterozygous, and that the watcher for mutants frequently seizes upon rare combinations of recessive features as a part of his elementary species?

But to breed true is only a secondary criterion of species. Inbred strains of domestic animals and plants do that to a certain degree. Varieties and races to a certain extent may do the same. The real criterion (and the one least often practically used by the systematist) is fertility within the group and sterility with other closely related groups. Here dogma holds sway among writers on organic evolution as well as among systematists, for we are told by those who have been accustomed since childhood to the idea of the objective reality of species that hybridization of species, that is, genuine species in good and regular standing before the scientific public, has played very little part in the origin of new species. This attitude was entirely logical in view of the accepted ultimate definition of a species. If the individuals of one species are actually sterile with members of another, hybridiza-

tion of species can not play an important part in the manufacture of new wild strains. But only in comparatively rare instances have attempts been made experimentally to mate Linnæan species. The dogma of the objective reality and uniform value of the species unit has diverted us from seriously attacking this problem. Just as in the nineteenth century the fixed idea of the immutability of species blocked the progress of the doctrine of evolution, so this dogma now stands in our way, and obstructs the possibility of vision. We need now fully to recognize the fact, which most biologists are ready to admit, that the term species is applied to most heterogeneous groups of individuals, groups of every conceivable size, based on differences that are most diverse in number and importance, often separated from allied groups entirely by the arbitrary judgment of the describer, and depending ultimately upon his personal temperament. These groups, as already stated, have been tested in comparatively few instances by the only reputable criterion that can be applied in the separation of closely allied groups, that of sterility or fertility *inter se*.

To one who tries to divest himself of the accepted ideas regarding species and is on the watch for evidence of hybridization among unlike strains that we are accustomed to call species, new cases of such hybridization frequently come to light. Especially is this true among the insects. In regions where the faunal areas of two "good" species overlap or are contiguous, such crossing not infrequently occurs.

A most interesting case is that of the four species of the coccinellid beetle *Adalia* that occur in the same region in Colorado, as worked out by Palmer.[4] These four forms with clean-cut differences in color and color pattern had been named and described by different authors as distinct species, yet three of them were found to be interbreeding with complete fertility but still respectively maintaining their identity, forming a regular Mendelian

[4] *Annals Entom. Soc. America*, IV, 3, September, 1911.

epistatic series: a red-brown spotless form, *melanopleura,* dominant at one end of the series, then *annectans,* a red-brown, spotted type, and finally the recessive, melanic, red-spotted *humeralis* with a color pattern different from that of *annectans* or of *Coloradensis,* another red-brown, spotted type of that locality. "But" says the upholder of the present idea of species, "here we have a single polymorphic species, not three or four different species. The breeding experiments show that the describers of these forms were wrong in ascribing systematic rank to mere color varieties." It goes, of course, almost without saying that the makers of these species did not before naming their beetles, breed them to determine whether they would breed true to type and were infertile *inter se.* Indeed, in how few cases has this been done! Even the larval stages of most known beetles are imperfectly unknown, much less the possible genetic relationship of one type to another, as determined by breeding them to maturity. Blaisdell[5] describes the case of two Californian Coccinellidæ which are found in winter in small groups under the bark of eucalyptus trees. "Usually there was one *Olla plagiata* with each of the groups [of *O. abdominalis*], irrespective of whether they were made up of two or more individuals." The same author, by selection of specimens of *abdominalis* representing different types of color pattern, describes its range of variation, but adds that his studies throw no light on the relationship of the two species. Had he bred certain individuals of *O. abdominalis* together, it is not at all unlikely, in view of his observation of the regular occurrence of a few *plagiata* in every group of *abdominalis,* that the former interbreeds with the latter and may be a simple recessive in respect to it. Miss Palmer's work on the allied *Adalia* certainly suggests this as a possibility.

Another remarkable case is that of the nine true-breeding species of grouse-locust, *Paratettix,* recently de-

[5] *Entom. News,* Vol. 24, No. 9, November, 1913.

scribed by Nabours.[6] These nine color types, or species, freely interbreed. The color pattern of the resulting F_1 hybrid in each case is a mosaic combination of those of the two parents. The latter in subsequent inbreeding may be extracted intact, each having been transmitted as a distinct unit, without dominance.

In Lepidoptera, an order in which polymorphism is notoriously common, hybridization between species has been frequently observed. Standfuss[7] devotes eight octavo pages of his excellent "Handbuch" simply to the enumeration of examples of such hybridization between palæarctic species of moths and butterflies, and acknowledges that he mentions only a fragment of all such cases on record or preserved in collections. This list would be greatly extended if American species were included. Seven different hybrid combinations within the genus *Colias* in the palæarctic region have been noted by Standfuss.

Colias philodice, the clouded sulphur or clover butterfly of the eastern and central United States, readily crosses with *C. eurytheme,* the orange sulphur or alfalfa butterfly of the western and central states. The territory of *philodice,* according to Scudder extends like a wedge westward from the Atlantic into the faunal area of *eurytheme.* Overlapping thus occurs in the Mississippi Valley, though *philodice* does not extend as far southward as the Gulf States, Texas, Louisiana and Mississippi, in which *eurytheme* is found.

These two species are fairly sharply distinguished by the difference in the ground color, which in *eurytheme* is orange, in *philodice* sulphur yellow. The middle spot of the upper side of the hind wing is brilliant orange in *eurytheme,* pale orange or yellow in *philodice.* The dark border of the hind wing of the female is wider in *eurytheme* than in *philodice* and broken with a row of large yellow spots.

6 *Journal of Genetics,* Vol. 3, No. 3, February, 1914.

7 "Handbuch d. paläarktischen Gross-Schmetterlinge," 1896, p. 51–53.

It has long been known that these two species hybridize in the Mississippi Valley, where both occur. By extended experiments during the past summer and previous autumn with *eurytheme* stock sent to me from Arizona through the kindness of Messrs. V. L. Wildermuth and R. N. Wilson and with *philodice* from New Hampshire, I have found that the two species mate together readily, and produce vigorous offspring. The species-hybrid males were then mated with *eurytheme* females, and more than half of the pairs (viz., four out of seven) were fertile. Mated together, however, the species-hybrids showed much sterility. Out of ten such matings, nine were infertile. From the tenth pair, nineteen adult butterflies were produced.

Orange in this cross is distinctly dominant over no orange, or yellow, but the color of the heterozygote is a pale orange overlying yellow, and is by no means as brilliant as the almost fiery orange of the large, summer seasonal variety, the typical "*eurytheme*." In broods emerging the last week in August and the first three weeks of September, when intense color may be expected, the heterozygote is pale orange, corresponding approximately to the variety known as *keewadin*, whereas those raised in the greenhouse and emerging early in December, resemble the small orange-yellow winter type known as *ariadne*. *Keewaydin*, according to Wright,[8] occurs at all seasons in California, though probably more abundantly in spring and autumn. Hence he regards this as the typical variety, rather than "*eurytheme*." It is intermediate, however, in size and intensity of color.

In general, therefore, there is an incomplete dominance of orange, the color of the heterozygote corresponding either to that of the intermediate or to that of the winter seasonal variety of *eurytheme*, depending upon the time of the year when, and the environmental condition under which, the cross is made. The wide, spotted margin of the hind wing in the female *eurytheme*, moreover, when pres-

[8] "Butterflies of the West Coast of the United States," p. 119.

ent in marked degree, is dominant over the narrower margin in *philodice.* This dominance of the orange manifests itself quite as distinctly if the albino female of *eurytheme,* instead of the orange female, is bred to the yellow *philodice* male. The daughters of such a family in one case (0, 1913) were 36 white, 35 orange; the sons, numbering 72, were, of course, all orange. The white species-hybrid (F_1) is identical in appearance with the albino *eurytheme,* the female color pattern of the latter (wide marginal bands) being dominant, and the orange middle spot both in pure bred albino *eurytheme* and in the albino hybrid being usually paler than in their orange sisters.

The second hybrid generation inbred (F_2) shows a well marked segregation of the sulphur-yellow color of *philodice,* as a simple Mendelian recessive. Three out of the sixteen colored (non-albino) individuals of the brood obtained in December, 1913, are definite recessives of clear sulphur yellow, with pale yellow middle spots on the hind wing. The most highly colored individuals are four that correspond in hue to pale examples of the light orange-yellow winter variety, *ariadne.* There is no return, at least in this winter brood (enclosed in a greenhouse in New Hampshire in December), to the brilliant orange of the grandparental *eurytheme* stock. Nor do they even return to the suffused light orange (intermediate) tint of the heterozygous father (*keewadin* type), for the ground color of all individuals of this brood (F_2) is *yellow,* either flushed or spotted, except in three individuals, with orange.

An interesting case of probable hybridization in the allied genus *Meganostoma,* or dog's head butterfly, is recorded by Wright[9] between the Californian *M. eurydice* and *M. cæsonia,* common throughout the southern states. The two species are remarkably different in color and have different food plants. The male of *eurydice* differs from that of *cæsonia* in having a violet luster and lacking

[9] *Loc. cit.*, p. 116.

the black border upon the hind wings possessed by *cæsonia*; in the female, *eurydice* is clear yellow with no dark border, while in *cæsonia* the female has a wide border similar to that of its male, though less well marked on the hind wings. The probable hybrid called *amorphæ* is a female, intermediate in color between the typical *cæsonia* and *eurydice*. That is, the border of *cæsonia* crossed with no border (if my interpretation is correct) is incompletely dominant. Wright says:

> At one time I was of the opinion that *Amorphæ* was a hybrid between *Eurytheme* and *Caesonia* . . . but of late years, as no male *Amorphæ* is known, I have concluded that *Amorphæ* is simply a dimorphic female [of *eurydice*].

Possibly it is both, an example of dimorphism produced either by immediate hybridization, or by a mutation resulting from some previous hybridization. That a male appears to be lacking in this case would not be an argument against the possibility of hybridization, for by such crossing the sex ratio is frequently upset, the product being of one sex only. But it appears to be possible that the male of this cross is that described as *M. bernardino*, a variety of *eurydice* found in the mountains of the same region where *amorphæ* also occurs. It is an interesting combination of the male coloration of both species, having the violet hue of *eurydice* that is lacking in *cæsonia* and having the dark border of the hind wings of *cæsonia* lacking in *eurydice*. Its female is described as being smaller than that of *eurydice*, but otherwise practically identical with it. This case, as Wright has suggested, is a most inviting subject for further study, and, judging by what he says of the sexual instincts of the *eurydice* male—"a wooer . . . energetic and persistent, not hesitating to ignore all rules of propriety, of species and of genera"—not difficult of experimental management.

The genus *Basilarchia*, the admiral butterflies, is well known for the hybridization of its very unlike species, *B. arthemis* the "banded purple" of the northern states,

B. astyanax the "red-spotted purple" of the southeastern states. The hybrid species, *B. proserpina,* occurs in a zone in which their two faunal areas overlap. In this same group is the common "viceroy" *B. archippus,* the range of which roughly covers that of both the other species and extends further westward, touching the Pacific coast in Washington (Scudder). The experiments of Edwards, and especially of Field, have shown that these three well-differentiated pure species occupying contiguous, or in respect to *archippus* overlapping, territory are in some cases at least mutually fertile. *B. arthemis* and *astyanax* regularly interbreed in the narrow zone where *proserpina* occurs. *Proserpina,* the hybrid, usually shows the general dominance of the *astyanax* characters (lack of white band).

From eggs laid by a wild female *proserpina* Edwards[10] secured three *arthemis,* one *proserpina.* Field[11] raised from a similar lot of eggs nine *proserpina,* seven *arthemis.* Presumably in each case the male parent was the recessive *arthemis,* and hence equal numbers of the two types would be expected. Field has also succeeded in crossing a ♀ *astyanax* with a ♂ *arthemis,* and a ♀ viceroy, *archippus,* with a ♂ *arthemis,* the latter pair producing nine males intermediate in color. Specimens of an apparent hybrid, intermediate in color between *astyanax* and *archippus,* have also occasionally been captured.

The complete overlapping of the faunal area of *archippus* upon those of the two other species indicates that, though crossing sometimes occurs, the resulting hybrids are probably usually sterile, though this matter has not yet been thoroughly investigated. *Proserpina,* however, is a fertile and extraordinarily variable hybrid. In view of its great variability it appears, by the way, not impossible that *archippus,* the red-brown "mimic" of the monarch, *Anosia plexippus,* may have arisen as a mutation from the hybrid *proserpina,* though the wide-spread

10 *Canadian Entomologist,* Vol. IX, 1877.

11 *Psyche,* Vol. XVII, No. 3, 1910.

range of *archippus* at present and our ignorance of the state of the *Basilarchia* stock at the time of the origin of the "mimic" make any such specific historical guess hazardous. It may, however, some time be possible by experimental breeding to extract from this red-spotted purple hybrid a red-brown type similar to *archippus*. If the *Basilarchia* stock were as easily bred as *Drosophila*, one might be very confident of accomplishing this. In any event, the theory of the origin of mimicry by natural selection is, in the opinion of the writer, entirely superfluous, though this celebrated monarch-viceroy case should be exhaustively studied by experimental methods, to determine whether natural selection now operates in any degree in the matter.

Examples of clusters of interbreeding types may be drawn in large numbers from various classes of animals and plants. Bateson[12] has recently called attention to the interesting case of the two American flickers described by Allen,[13] the eastern *Colaptes auratus* and the western and Mexican *C. cafer*, which hybridize in the zone in which their faunal areas overlap, the American grackles, the golden-winged and blue-winged warblers and their hybrids, Lawrence's and Brewster's warblers, and others.

In reference to the common purple grackle, which Chapman[14] regards as a hybrid between the Florida grackle and the bronzed grackle, Ridgeway[15] says:

> My own opinion in the matter exactly coincides with Mr. Chapman's but since so many forms now ranked as sub-species are similarly involved I prefer, at present, to leave the matter in abeyance.

This significant statement from a master of ornithological taxonomy indicates that hybridization among American birds is a promising subject for investigation.

Of the *occasional* mutual fertility of unlike strains different enough to be classed as unquestionable species.

[12] "Problems of Genetics," 1913, Chap. VII.

[13] *Bull. American Mus. Nat. Hist.*, Vol. IV, 1892.

[14] *Ibid.*

[15] "Birds of North and Middle America," Part 2, p. 219, 1902.

there also can be no doubt. "We can only escape the conclusion that some species are fully fertile when crossed," wrote Darwin,[16] "by determining to designate as varieties all the forms that are quite fertile," and he added that some plants exposed to unnatural conditions are so modified "that they are much more fertile when crossed by a distinct species than when fertilized by their own pollen."

The rareness of these crosses between unlike strains or species and the partial sterility of the offspring are not obstacles in the way of regarding occasional hybridization as one of the chief sources of mutation and hence eventually of new species, for, as my preliminary experiments in hybridizing species of *Colias* have already shown, there may exist within a strain of species-hybrids certain individuals that are fertile, though the most of their brothers and sisters, mated, respectively, in a similar way, are sterile. Nature probably makes more random experiments in hybridization than we imagine; many fail; some succeed; and in especially favorable stock like *Colias,* judging from the numbers of closely allied but different types (species) occurring in the same localities in western Asia or in northwestern United States and British America, probably many succeed.

In seeking to determine how mutation, whether the result of hybridization or of possible climatic influences, acts in the production of new species, it is possible from cases already at hand to suggest possible steps in the evolution of distinct, mutually infertile, types from one comparatively simple polymorphic species.

The well-known dimorphic European currant moth, *Abraxas grossulariata,* in which the light-colored (recessive) variety, *lacticolor,* is found in nature only in the female sex, will serve as an example of an elementary condition. *Lacticolor* males, as Doncaster[17] has shown,

16 "Animals and Plants under Domestication," Vol. II, Chap. 19, p. 179.

17 "Report of the Evolution Committee," 4, 1908.

may readily be bred. When one of these males is mated with a *lacticolor* female, there is produced in captivity a pure *lacticolor* strain. If *lacticolor* males and females should be segregated and allowed to breed together until they have become as abundant as the typical form, this case would then resemble that of the Colorado lady beetles of the genus *Adalia,* described above, in that it would consist of different types maintaining their identity while freely interbreeding with complete fertility. The *Abraxas* complex differs from the *Adalia* species-cluster, however, in the occurrence of sex-linkage in the inheritance of the *lacticolor* variety, whereas in *Adalia* the factors for the different color patterns apparently are distributed in the gametogenesis of a heterozygous individual without sex-linkage, freely and at random.

A more advanced stage in evolution is that represented by the *Basilarchia* species-cluster, in which partial sterility between the viceroy and the two purple species, over the faunal areas of which its own overlaps, and the difference in geographical distribution between the banded purple and red-spotted purple, keep the three elements apart.

By easy stages we may in imagination pass on to groups composed of closely allied species which sterility and local segregation completely separate from one another, groups that probably have arisen from a polymorphic species that has broken up into its constituent parts, and thus given rise to new elementary species.

The dimorphism of *Colias* differs from that of *Abraxas* in that the color of the rarer type of female can not be transferred in the ordinary course of breeding, without further mutation, to the male. It is a sex-limited character, like the female color pattern in *Colias,* (*i. e.,* a wide dark border broken with spots) and not sex-linked like the variety *lacticolor* of *Abraxas.*

The white female of *Colias* is regularly heterozygous for color. She produces as many white daughters as

yellow, or orange, as the case may be. Evidently, in order to extract a pure white race from *C. philodice* or *C. eurytheme,* it will be necessary by a mutation to obtain first a homozygous white female, and then by a further mutation a homozygous white male. White males are known in nature as rare aberrations, but, whether they are homozygous or heterozygous for color, it is impossible to say. Among the two thousand offspring of heterozygous white females of *philodice* and *eurytheme* that I have bred since 1908, there has been not a single white male. The sons of a white female, though some are capable of transmitting the white, are always yellow or orange. I have lately, however, raised a large brood in which all the females were white. This was a "back cross" between a white female of the orange *eurytheme* and a male species-hybrid (son of a white mother). Precisely similar matings, however, gave both white and colored female offspring in equal numbers; hence in the production of this brood there was probably a mutation. From such stock as this the extraction of a pure white race from *Colias* at some time may possibly be accomplished.

In this connection it is interesting to note that we have the testimony of a good observer, the late Mr. W. G. Wright,[17] who made the study of Californian butterflies his life work, to the effect that the white variety of *Colias eurytheme* "is now quite common, though twenty-five years ago it was a great rarity, and it was accounted a feat to secure one of them, and if the present rate of increase of the blond form shall go on, in a few hundred years the normal orange-colored female will be extinct and unknown." If this is a fact, and not an illusion due to a general increase in the population of *eurytheme* owing to an increase in the cultivation of the food plant, alfalfa, in that region, it may be the result of possible mutations, whereby homozygous white females may have been introduced into the population. It will be of inter-

[17] *Loc. cit.*, p. 117.

est to determine whether such true-breeding white females actually occur in California.

Evolution in *Colias* is usually regarded, on the other hand, as tending towards suppression of the white stock rather than its further extension, inasmuch as *Pieris* and other allied genera are white. It seems to be a reasonable hypothesis that, by progressive mutations in *Colias* affecting first the male then the female,[18] white has become yellow; yellow, orange; orange, red, or a fiery orange;[19] or yellow may be transmuted into black, as in an aberration of the male in *C. philodice.* By retrogressive or degressive mutations, accordingly, we may hope to isolate from *C. philodice* or *C. eurytheme* a pure white race.

Summary and Conclusions

The erroneous idea that Linnæan species are homogeneous, well-defined groups of equal importance has done much to retard progress in the experimental study of evolution. The limits of a species are often arbitrary, depending ultimately upon the temperament of the describer, and frequently based upon ignorance of the nearest allies of the individuals described, living in other parts of the world.

The most definite criteria of species, viz., that "specific" characters are constant, and that hybrids of Linnæan species are infertile *inter se,* are only approximately correct. Characteristics of species sometimes occur in heterozygous condition. Hybrids of Linnæan species, as has long been known, are often fertile. These matters, owing to traditional, unwarranted respect for described species, have received comparatively little investigation.

Examples of hybridization in *Adalia, Colias, Meganostoma, Basilarchia* and *Paratettix* among insects, in *Colaptes, Quiscalus,* and *Helminthophila* among birds are cited.

[18] In *C. dimera* of South America, for example, the female is yellow, but in the male the *fore wings* are orange.

[19] As in the Asiatic *eogene.*

Occasional fertile crossing of unlike strains that rarely interbreed is a probable source of mutations and new types.

A suggestion is made that a comparatively simple polymorphic species (like *Abraxas grossulariata*) may break up into a cluster of mutually fertile elementary species (*e. g.*, *Adalia* in Colorado). Further differentiation, involving partial sterility, may be illustrated by the *Basilarchia* species-cluster. This may be followed by the establishment, and isolation through complete sterility, of distinct types, or species in the strict sense of the term.

Evolution of color in the yellow and orange butterflies of the genus *Colias* involves white, which exists to-day in heterozygous condition in certain females. If the ancestors of *Colias* were white, as in Pierids generally, we have only to imagine a mutation in the male-producing germ cells of the original white females, by virtue of which white pigment was replaced by, or transmuted into, yellow. This would make all the males yellow, leaving all the females white, which is true of certain arctic species to-day.

A similar mutation affecting the germ cells of these white females, but introducing the factor for yellow into only half of them, would produce the heterozygous condition found in *C. philodice* and *C. eurytheme.* Pure yellow strains may readily be bred from such mixed stock, and hence, probably, it has come about that four fifths or nine tenths of the females of *C. philodice* in eastern United States are pure yellow.

Progressive mutations from yellow to orange and fiery orange, affecting first the male, then the female, have probably occurred in *Colias* in many part of the world, especially in warmer climates. Climatic conditions determine the amount of orange pigment in the cross between the orange *eurytheme* and the yellow *philodice.* This hybrid is larger and contains more orange when raised in summer than when bred in late fall and winter. *C. philodice* in this cross is a Mendelian recessive.

HEREDITY OF BRISTLES IN THE COMMON GREENBOTTLE FLY, LUCILIA SERICATA MEIG. A STUDY OF FACTORS GOVERNING DISTRIBUTION[1]

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In a previous paper[2] I have given data showing that variation in the number of posterior dorso-central and acrostichal bristles of the common greenbottle fly, *Lucilia sericata* Meig., is determined by hereditary factors. Since the publication of that paper further evidence, bearing upon the nature of the hereditary factors involved, has been obtained.

Two general conclusions from the work may be stated as follows:

1. Reduction in bristles tends to affect the males more than the females, while additional bristles are found more often in the females.

2. Distribution as well as number of bristles is hereditary.

On account of very high mortality in these flies it has been impossible to make selections as might seem desirable. The results, however, furnish considerable evidence for the foregoing conclusions, and throw light, I believe, on the nature of factors governing distribution, such as spotting factors, for example.

Fig. 1 shows the mesonotum of *Lucilia sericata* with chætotaxy normal. The bristles considered in my work are those lettered *A, B, C,* the post-acrostichals, and *A′, B′, C′*, the post-dorso-centrals.

[1] From the Entomological Laboratory of the Bussey Institution, Harvard University, No. 77.

[2] Whiting, P. W., "Observations on the Chætotaxy of Calliphorinæ," *Annals of the Entomological Society of America*, VI, 2.

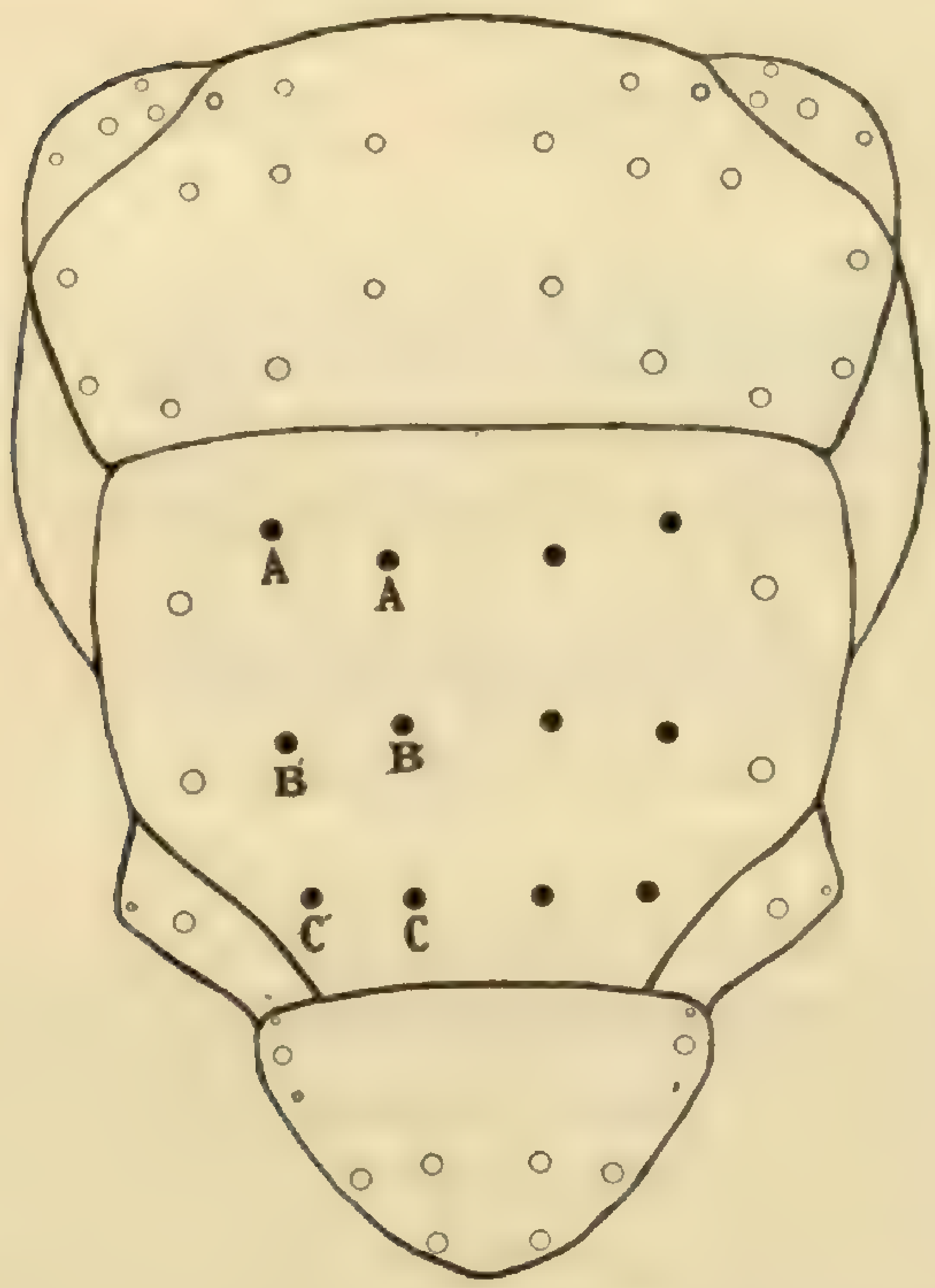

FIG. 1.

It is evident that these bristles form a group of twelve in four rows of three each.

This arrangement is recorded as 3, 3, 3, 3, the separation into rows being denoted by commas.

When one or two of the anterior bristles of a row are omitted, the row is denoted by 2 or 1, respectively.

In order to denote the omission of the second or third bristle when those anterior to it are not omitted, the normal positions of the bristles are recorded as a, b, c, from anterior to posterior. Thus a row lacking the second bristle would be called ac.

Addition of a supernumerary bristle into a row is denoted by ! inserted in the proper position between or in front of the letters denoting the normal bristles. Thus addition of a bristle in front of a row would be expressed by calling the row !abc.

Insertion of a supernumerary bristle between the normal rows is denoted by parentheses enclosing a, b, or c, acording to the position of the bristle from anterior to posterior. Thus a definition as 3, (a), 3, 3, 3, would denote the addition of a bristle between the first left post-dorso-central and the first left post-acrostichal.

Additional bristles are usually smaller than the normal, but range all the way from microchaetæ to the size of the normal macrochætæ. A small bristle is denoted by italics.

The progeny of a few wild females have been bred and counted since my previous paper.[3] These have been

TABLE I

Record of Flies Bred from Females Taken Wild

First generations only included here, hence not inbred. In the counts relating to reduction total absence of a bristle is counted as 1.0. A small-sized bristle is counted as a decrease of 0.5.

Mothers	Progeny from Flies Recorded in First Column																
	Number of Flies Showing Bristles						Total Progeny	Bristles Lacking in "Decreased" Flies								Bristles Added in "Increased" Flies	
	Normal		Decreased.		Increased.			Acrostichals						Dorso-centrals			
								1st		2d		3d					
	♂	♀	♂	♀	♂	♀		♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
12 normal flies	651	672	21	6	13	16	1,379	15	3	8	3	2	1	0	0	16	25
10 flies lacking 15 acrostichals (7 first, 6 second, and 2 third lacking)	258	289	30	7	3	3	590	16.5	5	15	3	1	0	1	0	4	3
4 flies having 7 bristles extra	154	125	2	5	10	8	304	0	1	1	4	0	1	0	0	11	9
Totals from 26 flies	1,063	1,086	53	18	26	27	2,273	31.5	9	24	10	3	2	1	0	31	37

Total males, 1,142. Number of bristles lacking in males 59.5.

Total females, 1,131. Number of bristles lacking in females, 22.

averaged with those recorded previously and the results given in Table I.

From this table it appears that progeny of normal mothers show a certain degree of variation in the direction both of loss and of acquisition of bristles; progeny of reduced mothers tend more toward reduction; and progeny of mothers bearing additional bristles tend more toward the addition of bristles. It is also evident that in

[3] It is thought desirable to put on record a detailed account of these families as they furnish in themselves a few points of interest. This record is given below with the exception of the progeny of 1913-*A*, discussed in a later part of this paper.

1913-*B*, *L. sericata* ♀ = 3, ab, ab, 3, taken at Bussey Institution, May 6, 1913, gave

11 ♂♂ = 3, 3, 3, 3.	
1 ♂ = 3, 3, 3, 2.	
3 ♂♂ = 3, 2, 3, 3.	17 ♀♀ = 3, 3, 3, 3.
1 ♂ = 3, 3, ac, 3.	1 ♀ = 3, 2, 3, 3.

1913-*C*, *L. sericata* ♀ = 3, 3, 2, 3, taken at Bussey Institution, May 6, 1913, gave

49 ♂♂ = 3, 3, 3, 3.	57 ♀♀ = 3, 3, 3, 3.
1 ♂ = 3, 3, *abc*, 3.	1 ♀ = *!*abc, a*!*bc, 3, 3.
1 ♂ = 3, a!bc, a!bc, 3.	1 ♀ = 3, a*!*bc, 3, 3.
1 ♂ = 3, a*!*bc, 3, 3.	
1 ♂ = 3, !abc, 3, 3.	

In this case I attribute the additional bristles to the combination of factors introduced by the male. An example of this sort in which a reduced female produces offspring abnormal predominantly by addition is very unusual. There are, however, occasionally flies with extra bristles in reduced strains, a fact which may be explained by recombinations of factors or by mutation.

1913-*F*, *L. sericata* ♀ = 3, 3, 3, 3, taken at Bussey Institution, March 19, 1913, gave

24 ♂♂ = 3, 3, 3, 3.	19 ♀♀ = 3, 3, 3, 3.

from a mating of these were produced

92 ♂♂ = 3, 3, 3, 3.	89 ♀♀ = 3, 3, 3, 3.
1 ♂ = 3, 3, a!bc, 3.	1 ♀ = 3, a!bc, 3, 3.

1913-*D*, *L. cæsar* ♀ = 3, 2, 2, 3 (the chætotaxy normal for this species), taken at Bussey Institution, May 5, 1913 gave

55 ♂♂ = 3, 2, 2, 3.	34 ♀♀ = 3, 2, 2, 3
4 ♂♂ = 3, 1, 2, 3.	1 ♀ = ac, 2, 2, 3.
1 ♂ = 3, 2, b, 3.	
2 ♂♂ = 3, 1, 1, 3.	
1 ♂ = 3, 2, 1, 3.	
1 ♂ = 3, b, 2, 3.	

The flies of this mating are not averaged with the others, as it is possible that this species may be different in its variability from *L. sericata*. It is noteworthy, however, that here also reduction favors the male more than the female.

general reduction tends considerably to favor the males, while addition favors the females to a slight extent.

In my previous paper (p. 264) is given in detail a record of the progeny of a female *L. sericata* (1912-c) lacking both of the first and the right second post-acrostichal (3, 2, 1, 3). These were inbred to the third generation, in all cases brother being mated with sister in an attempt to analyze the stock as thoroughly as possible and to reduce heterozygosis of factors.[4] Here again, due

[4] Mr. Harold D. Fish has kindly furnished me the following note:

"The importance of mating sisters with brothers for a long series of generations in the experiments aimed to detect Mendelizing units of inheritance and analyze groups of them, quite generally seems to have been overlooked. As first shown by Castle ('03), random mating of the individuals of successive generations beyond F_1 tends to produce in each generation a population with the same per cent. of homozygosis and heterozygosis as is present in the F_2 generation, *i. e.*, 25 per cent. of the individuals are homozygous for one factor of a given allelomorphic pair, 25 per cent. homozygous for the other factor, and 50 per cent. heterozygous for both. Such a system of random matings often has been confused with the more restricted system of mating sisters with brothers.

"It is evident that if *A* and *B* are an allelomorphic pair the F_2 zygotes, resulting from a mating of *AA* with *BB*, will be *AA*, 2*AB* and *BB*. Further, if these are all females and are mated in all possible ways with the same number and kinds of males, one sixteenth of the matings will be *AA* with *AA*, and one sixteenth will be *BB* with *BB*. One eighth of the matings, then, will be homozygous and produce only homozygous young, which, because of the restricted system of mating only sisters with brothers, will produce, in turn, only homozygous matings. The remaining matings, seven eighths of the total, will produce various proportions of homozygous and heterozygous offspring and matings. It is rather natural to assume that one eighth of these matings will be homozygous and seven eighths heterozygous. This would mean that the proportion of heterozygous matings between individuals of the F_n generation would be $(7/8)^{n-1}$. Accordingly one would expect an automatic increase in homozygosis. The expectation is justified although the figures are misleading.

"Dr. Raymond Pearl first published the figures exactly expressing the per cent. of automatic increase in homozygosis for paired allelomorphs, under the restriction of mating only sisters with brothers. This article appeared in the January, 1914, number of the AMERICAN NATURALIST. It is a correction of his paper in the October, 1913, number of the same periodical, in which he states in no uncertain terms that an automatic increase in homozygosis in obligate bisexual forms is impossible. When I read the October paper I was naturally much surprised, since, nearly a year before, during conversation with Mr. Whiting, the increasing per cent. of homozygous matings resulting from successive matings of sisters with brothers had been discussed. Of course, the per cent. of individuals in any generation, which are homozygous for one or the other of a pair of allelomorphs, is the same

to high mortality, selection as might have been desired has been impossible.

A detailed account of this strain is given in Table II. In recording any mating of this strain the letter *c* denoting the entire strain, is followed by F_1, F_2, etc., denoting the generation from which the mated flies have been chosen. This symbol is then followed by *a, b,* or *c,* denoting the first, second, or third mating, respectively, of the generation indicated. Thus mating cF_2b is the second mating of the second inbred generation of strain 1912—*c*. This method of recording matings has been followed throughout my work.

Several points of interest are to be noted in this strain but it is thought best to present the remaining data on reduced strains before proceeding to a discussion of this matter.

Strict inbreeding has been followed in the strain recorded below. In no case have there been either cousin-matings or outcrossings.

1913-*A*, *L. sericata* ♀ = 3, ac, ac, 3, taken at Bussey Institution, Forest Hills, Mass., May 6, 1913, gave

F_1

96 ♂♂ = 3, 3, 3, 3.	129 ♀♀ = 3, 3, 3, 3.
1 ♂♂ = 3, ac, ac, 3.	1 ♀ = 3, ac, 3, 3.
2 ♂♂ = 3, ac, 3, 3.	2 ♀♀ = 3, 2, 3, 3.
2 ♂♂ = 3, 3, ac, 3.	
1 ♂ = 3, 2, ac, 3.	
4 ♂♂ = 3, 2, 3, 3.	
3 ♂♂ = 3, 3, 2, 3.	

as the per cent. of the allelomorphic factors which are homozygous in the average individual of that generation. Because Dr. Pearl in his October paper referred frequently to the paper by Dr. E. M. East ('12) on "Heterozygosis in Evolution and Plant Breeding." I gave Dr. East my figure expressing the per cent. of homozygosis in successive generations resulting from matings of sisters with brothers. Dr. Pearl's correction followed a letter from Dr. East which pointed out the error of applying the mathematics of random matings in each generation to a case where sisters always had been mated with brothers. The percentages, as computed, were published by Dr. Pearl for the following generations: P_1—100 per cent., F_1—0 per cent., F_2—50 per cent., F_3—50 per cent., F_4—62.5 per cent., F_5—68.25 per cent., F_6—75 per cent., F_7—79.687 per cent., F_8—83.594 per cent, F_9—86.719 per cent., F_{10}—89.258 per cent. Previous to giving these figures to Dr. East I computed the number of generations necessary to reduce heterozygosis to less than one half of one per cent. and found this condition first realized in the F_{25} generation, which is 99.553 per cent. homozygous. The importance of these figures in work of this nature is quite obvious."

TABLE II

RECORD OF STRAIN 1912*c*, *L. sericata* ♀ (3, 2, 1, 3), TAKEN AT THE GARBAGE SCOW, BOSTON, AUGUST 8, 1912

Generations and Character of Matings	Progeny from Matings Recorded in First Column																	
	Number of Flies Showing Bristles						Total Progeny	Bristles Lacking in "Decreased" Flies								Bristles Added in "Increased" Flies	
	Normal		Decreased		Increased			Acrostichals						Dorso-centrals			
								1st		2d		3d					
	♂	♀	♂	♀	♂	♀		♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
F_1 from mother = (3, 2, 1, 3)	10	12	0	0	0	0	22	0	0	0	0	0	0	0	0	0	0
F_2 from cF_1a = normal pair	10	7	0	0	0	0	17	0	0	0	0	0	0	0	0	0	0
F_2 from cF_1b = normal pair	42	39	2	2	2	0	87	1	0	0	3	0	0	2 (2d)	0	2	0
F_2 from cF_1c = normal pair	55	62	10	9	1	0	137	16	7	0	1	0	1	1 (2d)	1 (1st)	1	0
F_3 from cF_2a = normal male × 2 normal females	163	170	6	6	2	7	354	1	0	4	2	0	0	0	4 (1st) 3.5 (2d) 2 (3d)	2	8
F_3 from cF_2b = normal pair	92	85	0	1	11	4	193	0	0	0	1	0	0	0	0	13	4
Totals	372	375	18	18	16	11	810	18	7	4	7	0	1	3	10.5	18	12

F_2

from AF_1a = { ♂ = 3, ac, 3, 3. ♀ = 3, 2, 3, 3. }

24 ♂♂ = 3, 3, 3, 3.
11 ♂♂ = 3, ac, ac, 3.
13 ♂♂ = 3, ac, 3, 3.
9 ♂♂ = 3, 3, ac, 3.
2 ♂♂ = 3, a*b*c, ac, 3.
1 ♂ = 3, 3, a*b*c, 3.
1 ♂ = 3, 1, 1, 3.
3 ♂♂ = 3, ac, 2, 3.
5 ♂♂ = 3, 2, ac, 3.
1 ♂ = 3, 2, 2, 3.
5 ♂♂ = 3, 2, 3, 3.
2 ♂♂ = 3, 3, 2, 3.
1 ♂ = 3, acc, 3, 3.

53 ♀♀ = 3, 3, 3, 3.
2 ♀♀ = 3, ac, ac, 3.
5 ♀♀ = 3, 3, ac, 3.
1 ♀ = 3, ac, a*b*c, 3.
1 ♀ = 3, ac, 2, 3.
2 ♀♀ = 3, 3, a*b*c, 3.
1 ♀ = 3, a*b*c, 3, 3.
1 ♀ = 3, a*b*c, 2, 3.
2 ♀♀ = 3, 2, 2, 3.
1 ♀ = 3, 3, 2, 3.
1 ♀ = 3, 3, a*!!*c, 3, 3.
1 ♀ = 3, a!bc, 3, 3.

F_3

from AF_2a = ♂ and ♀ = 3, ac, ac, 3. Pair segregated July 12; larvæ July 25.

♂♂	♀♀	
6	35	= 3, 3, 3, 3.
42	18	= 3, ac, ac, 3.
9	18	= 3, ac, 3, 3.
16	12	= 3, 3, ac, 3.
5	2	= 3, ac, 2, 3.
7	2	= 3, 2, ac, 3.
10	4	= 3, 2, 2, 3.
7	7	= 3, 2, 3, 3.
5	7	= 3, 3, 2, 3.
1	0	= 3, ac, a, 3.

from AF_2b =
♂ = 3, ac, 2, 3.
♀ = 3, a*b*c, 2, 3.
Pair segregated July 12; larvae July 25.

♂♂	♀♀	
16	45	= 3, 3, 3, 3.
34	9	= 3, ac, ac, 3.
8	9	= 3, ac, 3, 3.
7	11	= 3, 3, ac, 3.
8	0	= 3, ac, 2, 3.
9	1	= 3, 2, ac, 3.
3	0	= 3, 2, 2, 3.
2	1	= 3, 2, 3, 3.
4	1	= 3, 3, 2, 3.
0	1	= 3, a*b*c, ac, 3.
0	3	= 3, 3, a*b*c, 3.
0	3	= 3, a*b*c, a*b*c, 3.
1	0	= 3, b, 3, 3.
1	0	= 3, ac, a*b*c, 3.
0	1	= 3, a*b*c, 3, 3.

F_4

from AF_3a = { ♂ = 3, ac, a, 3, from AF_2a. Pair segregated August 14; ♀ = 3, ac, ac, 3, larvæ August 20. }

♂♂	♀♀	
6	32	= 3, 3, 3, 3.
24	11	= 3, ac, ac, 3.
4	20	= 3, ac, 3, 3.
6	13	= 3, 3, ac, 3.
9	6	= 3, ac, 2, 3.
6	7	= 3, 2, ac, 3.
3	4	= 3, 2, 2, 3.
4	7	= 3, 2, 3, 3.
1	5	= 3, 3, 2, 3.
1	0	= 3, ac, 1, 3.
0	1	= 3, ac, 3, 3.
1	0	= 3, ac, bcc, 3.
0	1	= 2, 2, 2, 3.
0	1	= 3, 3, a*bb*c, 3.

from AF_3b = ♂ and ♀ = 3, 2, ac, 3, from AF_2a. Pair segregated August 13; larvæ August 20.

♂♂	♀♀	
0	18	= 3, 3, 3, 3.
10	3	= 3, ac, ac, 3.
4	5	= 3, ac, 3, 3.
1	2	= 3, 3, ac, 3.
13	3	= 3, ac, 2, 3.
13	2	= 3, 2, ac, 3.
6	2	= 3, 2, 2, 3.
1	7	= 3, 2, 3, 3.
1	4	= 3, 3, 2, 3.

from AF_3c = ♂ and ♀ = 3, 2, 2, 3, from AF_2a. Pair segregated August 13; larvæ August 25.

♂♂	♀♀	♂♂	♀♀
6	15 = 3, 3, 3, 3.	2	15 = 3, 2, 3, 3.
10	7 = 3, ac, ac, 3.	3	8 = 3, 3, 2, 3.
11	7 = 3, ac, 3, 3.	0	1 = ac, 1, 2, ac.
10	12 = 3, 3, ac, 3.	1	0 = 3, 2, acc, 3.
8	3 = 3, ac, 2, 3.	2	1 = 3, acc, ac, 3.
7	7 = 3, 2, ac, 3.	1	0 = 3, acc, 3, 3.
5	4 = 3, 2, 2, 3.		

from AF_3d = ♂ and ♀ = 3, ac, ac, 3, from AF_2a. Pair segregated August 13; male died August 18 and another with same chætotaxy put in; larvæ September 1.

♂♂	♀♀	♂♂	♀♀
0	3 = 3, 3, 3, 3.	1	1 = 3, ac, 2, 3.
1	2 = 3, ac, 3, 3.	1	0 = 3, 3, aabc, 3.
1	1 = 3, 3, ac, 3.		

The record of 1913-*A*, recorded in tabular form is given in Table III.

We are now in a position to consider the nature of reduction of bristles in *Lucilia sericata*.

It is evident from Table I (record of first generation flies), that reduction and addition of bristles are both hereditary. It is further evident from Table III, (inbred strain), that reduction yields readily to selection. This effect may be expressed by making the number of bristles lost the numerator of a fraction of which the denominator is the number of bristles normal. We then have a ratio for each generation of 1913—*A* as follows:

$$F_1 \cdot \frac{18}{2892} = 0.006 \pm .010, \qquad F_3 \cdot \frac{435}{4692} = 0.093 \pm .003,$$

$$F_2 \cdot \frac{99}{1788} = 0.055 \pm .004, \qquad F_4 \cdot \frac{532.5}{5100} = 0.104 \pm .003.$$

It may be readily seen by glancing at these figures that selection has a very rapid effect. It also appears that as we pass from F_1 to F_4 the effect of selection gradually diminishes. This may be expressed by dividing the above decimals for each generation by that of the preceding generation.

$$\frac{F_2}{F_1} = \frac{0.055}{0.006} = 9.16, \qquad \frac{F_3}{F_2} = \frac{0.093}{0.055} = 1.69,$$

$$\frac{F_4}{F_3} = \frac{0.104}{0.093} = 1.11.$$

The reason for this decrease in the effect of selection in the later generations is that as the selection advances the majority of the flies become reduced in two bristles only.

TABLE III

RECORD OF STRAIN 1913-*A*, *L. sericata* ♀ (3, ac, ac, 3) TAKEN AT THE BUSSEY INSTITUTION, FOREST HILLS, MASS., MAY 6, 1913

Generations and Character of Matings	Progeny from Matings Recorded in First Column																		
	Number of Flies Showing Bristles						Decreased and Increased in Same Individual		Total Progeny	Bristles Lacking in "Decreased" Flies								Bristles Added in "Increased" Flies		Small 2d Acrostichals
	Normal		Decreased		Increased					Acrostichals						Dorsocentrals				
										1st		2d		3d						
	♂	♀	♂	♀	♂	♀	♂	♀		♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
F_1 from mother = (3, ac, ac, 3)	96	129	13	3	0	0	0	0	241	8	2	7	1	0	0	0	0	0	0	0
F_2 from AF_1a = {♂ = 3, ac, 3, 3, ♀ = 3, 2, 3, 3	24	53	53	16	0	1	1	1	149	19	7	58.5	14.5	0	0	0	0	1	2	8
F_3 from AF_2a = ♂ and ♀ = 3, ac, ac, 3	6	35	102	70	0	0	0	0	213	34	26	123	70	1	0	0	0	0	0	0
F_3 from AF_2b = {♂ = 3, ac, 2, 3, ♀ = 3, *abc*, 2, 3	16	45	77	40	0	0	0	0	178	30	3	101.5	45.5	1	0	0	0	0	0	12
F_4 from AF_3a = {♂ = 3, ac, a, 3, ♀ = 3, ac, ac, 3, from AF_2a	6	32	58	75	0	0	1	1	173	28	36	76	69.5	0	0	0	1 (1st)	1	0	2
F_4 from AF_3b = ♂ and ♀ = 3, 2, ac, 3 from AF_2a	0	18	49	28	0	0	0	0	95	40	20	51	18	0	0	0	0	0	0	0
F_4 from AF_3c = ♂ and ♀ = 3, 2, 2, 3, from AF_2a	6	15	56	64	0	0	4	1	146	31	43	62	46	0	0	0	2 (2d)	4	1	0
F_4 from AF_3d = ♂ and ♀ = 3, ac, ac, 3, from AF_2a	0	3	3	4	1	0	0	0	11	1	1	3	4	0	0	0	0	1	0	0
Totals	154	330	411	300	1	1	6	3	1,206	191	138	482	268.5	2	0	0	3	7	3	

Rarely does a fly occur lacking more than two. In the few cases in which three or more bristles are lacking, the absence of the third acrostichals or of the dorso-centrals is as frequent as the absence of first and second acrostichals. Why this should be is difficult to understand, as it would be expected that both first and both second post-acrostichals might frequently be lacking in the same fly, especially as flies asymmetrical for the loss of these bristles are common.

A further point of interest lies in the fact that not only is *number* of bristles a hereditary matter, but their *distribution* is also hereditary. Thus from Table I (first-generation flies) we see that in general the first post-acrostichals tend to be reduced more than the second. This may be expressed as a fraction:

$$\frac{\text{First post-acrostichals lacking}}{\text{Second post-acrostichals lacking}} = \frac{40.5}{34} = 1.19.$$

It is possible that this tendency to reduce the first post-acrostichal more than the second is evidence of relationship to *L. cæsar* Linn., in which the absence of the former and the presence of the latter is the normal condition. Strain 1913—*A* (Table III), however, gives

$$\frac{\text{First post-acrostichals lacking}}{\text{Second post-acrostichals lacking}} = \frac{329}{750} = 0.43.$$

Considering the reduction in the first post-acrostichals separately, we may express the effect of selection as follows:

Parents. Matings.	1st post-acros. lacking.	Offspring. $\frac{\text{First post-acros. lacking.}}{\text{First post-across. normal (2 per fly)}}$.
A	0(?)	$\frac{10}{482} = 0.021 \pm .004.$
AF_1a	1	$\frac{26}{298} = 0.087 \pm .011.$
AF_2a	0	$\frac{60}{426} = 0.141 \pm .002.$
AF_2b	2	$\frac{33}{356} = 0.093 \pm .010.$

AF_3a	0	$\frac{64}{346}=0.185\pm.014.$
AF_3b	2	$\frac{60}{190}=0.316\pm.023.$
AF_3c	4	$\frac{74}{292}=0.253\pm.017.$

From these figures it is readily seen that reduction in the first post-acrostichals is not entirely consistent with the direction of selection.

Let us test the same matter for reduction in the second post-acrostichals.

Parents Matings	1st post-acros. lacking	Offspring. First post-acros. lacking. / First post-acros. normal (2 per fly)
A	2(?)	$\frac{8}{482}=0.017\pm.004.$
AF_1a	1	$\frac{63}{298}=0.211\pm.016.$
AF_2a	4	$\frac{193}{426}=0.453\pm.016.$
AF_2b	1.5	$\frac{147}{356}=0.413\pm.018.$
AF_3a	4	$\frac{145.5}{346}=0.420\pm.179.$
AF_3b	2	$\frac{69}{190}=0.363\pm.023$
AF_3c	0	$\frac{108}{292}=0.370\pm.019.$

In this case also the results are not consistent with the direction of selection, although there is better agreement here than in the case of the first post-acrostichals. This is probably due to the fact that the numbers are larger. As regards the irregularities that do occur, I consider them as evidence of recombinations of multiple factors, insofar as they are not due to probable error.

1912—*c* (Table II) is a strain that especially tends to lack the first post-acrostichals. Thus for the entire strain

$$\frac{\text{First post-acrostichals lacking}}{\text{Second post-acrostichals lacking}}=\frac{25}{11}=2.27.$$

In the 137 offspring of a single mating of this strain, $c\mathrm{F}_1c$, there are 23 first post-acrostichals lacking, showing that it is due to this mating especially that the strain is so lacking in first post-acrostichals.

It can not as yet be said that the factors governing the first post-acrostichals are altogether independent of those governing the second. That a certain degree of independence obtains is evident from a comparison of the ratio of reduction in first to reduction in second post-acrostichals in flies in general (Table I), with the same ratio for strain 1913—*A*. In the former case we have 40.5/34 or 1.19. In the latter we have 329/750, or 0.43. In order to establish the independence of the factors underlying these two tendencies it will be necessary to obtain, either by selection from a strain showing both tendencies or by breeding from wild stock, two strains, one tending to lack the first while retaining the second, and the other tending to lack the second while retaining the first.

A point of interest in strain 1913—*A* is the presence of twelve small second post-acrostichals in the progeny of $A\mathrm{F}_2b$ in which the female had one of these reduced to half size. The progeny of $A\mathrm{F}_2a$ in which there was total absence of these bristles showed either presence or absence of the same but no reduced bristles. In F_2, however, we have eight reduced bristles. The occurence of these small bristles in the progeny of certain matings is taken as an indication of recombinations of multiple factors, but the numbers are too small to establish this with certainty.

A glance at the tables shows that third post-acrostichals are rarely lacking. These are normally present in all related species, while in a few,—*Cynomyia mortuorum, Musca domestica, Pseudopyrellia cornicina,* and others, there is normally but one post-acrostichal, and this is always the last.

Posterior dorso-centrals are very rarely absent. Thus in the 2,273 flies recorded in Table I only one had a single post-dorso-central missing. Reduction in post-acrosti-

chals among these is 79.5. Among the 1,206 flies of strain 1913—*A* there are but three post-dorso-centrals gone. This latter is a highly reduced strain as regards post-acrostichals, lacking 1,081. This great reduction in acrostichals seems not appreciably to have affected the dorso-centrals, a fact which argues for the independence of the factors controlling the distribution of these two sets of bristles.

Thus for flies recorded in Table I we have

$$\frac{\text{Post-acrostichals lacking}}{\text{Number of Flies}} = \frac{79.5}{2273} = 0.03.$$

One post-dorso-central lacking.

For flies in strain 1913—*A* (Table III) we have

$$\frac{\text{Post-acrostichals lacking}}{\text{Number of Flies}} = \frac{1081}{1206} = 0.89.$$

Three post-dorso-centrals lacking.

Among the 3,238 flies recorded in Tables I and III only four post-dorso-centrals are lacking, while among the 810 flies of strain 1912—*c* (Table II) there are 13.5 lacking. The lack of post-acrostichals in this latter strain is 37. There are 9.5 dorso-centrals lacking in the progeny of the trio, cF_2a, among which there are only seven post-acrostichals lacking.

Thus we see that lack of post-dorso-centrals is in no way correlated with lack of post-acrostichals, but is evidently governed by distinct factors.

VARIATION BY ADDITION OF BRISTLES

A strain of *Lucilia sericata*, 1913—*E*, showed some interesting variations chiefly in the direction of addition of bristles. The mother was normal (3, 3, 3, 3), taken at the Bussey Institution, March 19, 1913. The detailed account of the strain follows:

F_1

♂♂	♀♀	
38	43	= 3, 3, 3, 3.
1	0	= 3, 3, ab!c, 3.

F_2

from EF_1a = { ♂ = 3, 3, ab!c, 3.
♀ = 3, 3, 3, 3.

♂♂	♀♀
69	76 = 3, 3, 3, 3.
1	0 = ab!c, 3, 3, 3.
0	1 = !abc, 3, 3, !abc.

F_3
from EF_2a = ♂ and ♀ = 3, 3, 3, 3.

♂♂	♀♀	♂♂	♀♀
318	251 = 3, 3, 3, 3.	4	5 = 3, a!bc, 3, 3.
13	51 = !abc, 3, 3, !abc.	0	1 = !a!bc, 3, 3, !abc.
1	4 = !abc, 3, 3, 3.	1	0 = 3, abc!, abc!, 3.
6	6 = 3, 3, 3, !abc.	1	0 = !abc, a!bc, a!bc, !a
1	3 = 3 (a), 3, 3, 3.	0	1 = !abc, a!bc, 3, !abc
5	2 = 3, 3, 3 (a), 3.	1	0 = 3, ab!c, 3, 3.
3	5 = 3, 3, a!bc, 3.	1	1 = a!bc, 3, 3, a!bc.
1	0 = 3, a!bc, abc!, 3.	0	3 = !abc, 3, 3, !a!bc.
1	0 = 3, 3, 3, a!bc.	0	1 = 3, a!bc, 3, !abc.
1	0 = 3, 3, 3, ab!c.	0	1 = !abc, 3, 3 (a), !abc
1	0 = !abc, a!bc, 3, 3.	0	1 = !abc, a!bc, 3, !a!bc
1	0 = 3, 3, 3 (b), 3.	0	1 = a!bc, 3, a!bc, a!bc.
1	1 = 3, a!bc, a!bc, 3.	1	0 = !bc, 3, 3, !a!bc.
1	0 = !a!bc, !a!bc, !a!bc, !a!bc.	1	0 = 3, 3, 2, 3.
0	1 = 3 (b), 3, a!bc, a!bc.	1	0 = 3, ac, 3, 3.
0	2 = !a!bc, 3, 3, !abc.	1	0 = 3, ac, ac, 3.
0	1 = !abc, 3, a!bc, !abc.	0	1 = 3, abc, 3, 3.

F_4
from EF_3a = { ♂ = 3, 3, 3, 3. ♀ = 3, 3, a!bc, 3. }

Pair segregated, July 22; larvæ July 30.

♂♂	♀♀	♂♂	♀♀
191	100 = 3, 3, 3, 3.	1	0 = !abc, 3, abc!, !abc.
25	43 = !abc, 3, 3, !abc.	2	0 = 3, abc!, 3, 3.
4	3 = !abc, 3, 3, 3.	1	0 = !abc (a), 3, 3.
0	1 = 3, 3, 3, !abc.	1	0 = 3 (a), 3, 3 (a), 3.
0	1 = !abc, a!bc, 3, !abc.	1	1 = !abc, 3, 3 (a), !abc.
1	2 = !abc, 3, a!bc, !abc.	0	1 = !bc, 3, 3, 3.
0	2 = !abc, a!bc, a!bc, !abc.		

from EF_3b = ♂ and ♀ = 3, 3, 3, 3. Pair segregated August 22.

♂♂	♀♀	♂♂	♀♀
41	57 = 3, 3, 3, 3.	2	0 = 3, a!bc, 3, 3.
0	1 = 3, a!bc, 3, !abc.	0	1 = !abc, 3, 3, !abc.
1	0 = 3, abc!, 3, 3.	0	1 = !abc, a!bc, a!bc, !abc.

A summary of this strain is given in Table IV.

The points of interest to be noted in this table are as follows:

There are many supernumerary bristles in the flies of this strain.

The number of bristles added in the progeny of any mating is very variable and has no consistent relation to the visible character of the parents.

Addition of bristles tends very much to favor the females, reduction still affecting the males.

Despite the high ratio of bristles added, there are

TABLE IV

RECORD OF 1913-*E* STRAIN, *L. sericata* ♀ (3, 3, 3, 3) TAKEN AT THE BUSSEY INSTITUTION, FOREST HILLS, MASS., MARCH 19, 1913

Generation and Character of Matings	Progeny from Matings Recorded in First Column												
	Number of Flies Showing Bristles								Total Progeny	Bristles Lacking in "Decreased" Flies.		Bristles Added in "Increased" Flies	
	Normal		Decreased		Increased		Decreased and Increased						
	♂	♀	♂	♀	♂	♀	♂	♀		♂	♀	♂	♀
F_1 from mother = (3, 3, 3, 3)	38	43	0	0	1	0	0	0	82	0	0	1	0
F_2 from EF_1a = { ♂ = 3, 3, ab ! c, 3, ♀ = 3, 3, 3, 3	69	76	0	0	1	1	0	0	147	0	0	1	2
F_3 from EF_2a = normal pair	318	251	3	1	44	91	1	0	709	4	0.5	75	170
F_4 from EF_3a = { ♂ = 3, 3, 3, 3, ♀ = 3, 3, a ! bc, 3	191	100	0	0	36	53	0	1	381	0	1	73	111
F_4 from EF_3b = normal pair	41	57	0	0	3	3	0	0	104	0	0	3	8
Totals	657	527	3	1	85	148	1	1	1,423	4	1.5	153	291

nevertheless a few flies in the strain in which bristles are lacking.

Bristles normally present may be lacking in individuals having additional bristles.

General Summary and Conclusions

Taking a general summation of all the bred material of *Lucilia sericata,* we find that reduction affects the males while addition affects the females. Of the 5,367 flies bred, 2,708 are males and 2,659 are females, giving practical equality.

Reduction in the males is 748.5 bristles, while in the females it is only 455.5 bristles. As has been noted before the degree of reduction in the females is increased by the later generations of strain 1913—*A,* by reason of the fact that reduction rarely goes beyond the loss of two bristles in a single fly. Thus when most of the flies of a population become reduced to this extent it is evident that reduction in the males would be but slightly in advance of that in the females.

There are 210 bristles added in the males, while there are 343 added in the females. Thus addition affects the females more than the males. These figures for bristles added represent number of bristles, and thus no distinction is made between bristles of large and bristles of small size.

I wish to express my appreciation for the advice and criticism offered me in this work by Professor W. M. Wheeler, Messrs. H. D. Fish, S. G. Wright, and C. C. Little.

PHYSIOLOGICAL CORRELATIONS AND CLIMATIC REACTIONS IN ALFALFA BREEDING[1]

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Climatic Reactions

To the worker who attempts to apply the recognized laws of heredity to the actual operations of plant improvement many difficulties arise which heretofore have been largely avoided by students of pure genetics. Color and form characters are but little affected by the immediate ordinary environment and hence, for the sake of simplicity, are usually chosen by investigators of heredity. To the economic breeder, however, such characters are of but little consequence except in so far as they indicate phyletic relationships. Of greater importance to the breeder are those differences in yield and quality which are the results of inherited, invisible, physiological powers within the plants, whereby each variety may respond differently in manner or degree to the same environmental stimulus.

Those hereditary units which have to do with vegetative vigor, heat, cold and drought resistance, time of maturity, chemical structure, reproductive strength, etc., are as yet but little understood. This is largely due to the difficulty of exact experiments concerning them. This difficulty is occasioned by the complexity of the reactions of these hereditary forces with the external environment, and also by the direct influence of the development of one part of the plant upon that of some other part. The plant at maturity presents the resultant of its environmental reactions during development. The nature of these reactions

[1] Read before the American Breeders' Association, Columbia, S. C., January 26, 1913.

is determined by the structure of the vital forces within. These differences in vital structure may or may not be accompanied by visible morphological differences. Such cases of correlation have been known and used in selecting for qualities which they were thought to indicate. The much quoted example of the supposed correlation between the short-haired rachilla and high brewing quality in barley is a case in point. It has been found, however, that, whereas, in one strain or race the correlation may hold, in another, the two characters are in no way related. Another case of similar nature is the coupling of cob and pericarp color in certain varieties of corn and their complete independence in others. Many other examples could be adduced to show that the coupling of two characters in a given race of plants is no indication that these same characters are inseparably linked in all races of the same species. These facts have greatly reduced the value formerly ascribed to gametic correlations in plant breeding. Under our present knowledge, therefore, we must depend, for the most part, upon direct experimentation, rather than correlations, to discover the hereditary physiological characters of the varieties with which we are working. Any additional light, therefore, which may be had concerning the nature of such characters, together with methods for the study of the behavior of the same in their relation to each other and to their physical surroundings, will have not only a scientific value, but will also fill a distinct practical need.

As an illustration of such a study we may now examine the data concerning the development, yield and chemical composition of forty-four regional varieties of alfalfa which were grown on the Experiment Station Farm at Phoenix, Arizona, during the season of 1910. In the case of this plant, which occupies the ground throughout the year and from which six or seven crops may be harvested during the growing period, the climatic factors include a long series of variations coincident with the changing seasons. Now, since every variety consists of its own pecul-

iar complex of hereditary physiological forces, each sensitive in its own manner and degree to the impinging external stimuli, it is not surprising that the resultant (the gross climatic reaction) should be sharply different in the several varietal groups.

The unequal effects upon the vegetative growth of the different varieties brought about by the climatic changes which occurred during the course of the summer may be exhibited by calculating the place variation in yield. This is best shown by correlating the first with each of the following cuttings throughout the season. The result is a definite curve, beginning and ending high with a strong sag in the middle.

TABLE I

PLACE VARIATION IN YIELD

Cuttings	1 and 2	1 and 3	1 and 4	1 and 5	1 and 6
Correlation.	+ .75 ± .04	+ .68 ± .05	+ .33 ± .09	+ .36 ± .09	+ .58 ± .07.

These figures indicate the presence of some disturbing factor which reached its maximum intensity during the fourth and fifth cuttings, and to which certain plots were more sensitive than others. The average period through which the growth of these two crops extended was June 22 to August 27. The fact that these dates include the hottest portion of the summer strongly suggests temperature as the disturbing factor.

The mean maximum temperature, mean minimum relative humidity and the correlation between yield and water supplied are given in the following table:

TABLE II

TEMPERATURE, RELATIVE HUMIDITY AND WATER SUPPLY

Cutting	Dates Including Average Periods of Growth	Mean Maximum Temperature ° F.	Mean Minimum Relative Humidity	Correlation Between Yield and Water Supply
1	From March 23 to April 23	82.8	27.00	
2	From April 23 to May 23	93.8	23.00	— .09 ± .10
3	From May 23 to June 22	103.6	20.40	+ .05 ± .10
4	From June 22 to July 23	104.8	25.26	+ .40 ± .09
5	From July 23 to August 27	104.4	30.00	+ .21 ± .10
6	From August 27 to October 5	102.0	25.18	— .04 ± .10

That the relative humidity had little to do with yield is shown by the fact that the highest averages for this factor occurred on the first and fifth cuttings which were the highest and lowest in yield, respectively.

Although it was intended to give each plot approximately the same amount of water for each cutting, unevenness in the slope made this impossible. The average amount of water applied to each cutting was 6.28 inches with an average standard deviation of 1.54 inches. Now, taking cognizance of this variation in the water supply, we find that its effect upon the yield was only appreciable in the fourth and fifth cuttings. Records were not made of the water supplied to the first cutting, but after that time they are complete. By reference to Table II it will be observed that these correlations in the second, third and sixth cuttings are so small as to be negligible, but in the fourth and fifth cuttings they are sufficiently large to indicate that this factor was of some importance in governing the yields. These results may be interpreted as meaning that approximately 6.28 inches of water were ample for each cutting during the cooler weather of spring and fall. That too much was not given at these seasons, however, is shown by the absence of large minus correlations. Factors other than water supply, therefore, governed the yields during these periods. Hot, dry weather came on during the growth of the third cutting, but the amount of water supplied plus the winter and spring surplus left in the soil was ample to mature the crop. With the continued high demand for water during the hot weather of July and August, the surplus having been exhausted and the summer rains helping but little, six and one fourth inches was not sufficient. There was, therefore, marked suffering for water, which was reflected in the yields of those plots that received slightly more or less of irrigation than the others.

It would seem, therefore, that high temperature and a slight deficiency of water were the disturbing factors in

the relative yields of the varieties tested, and that certain ones were more sensitive than others to these influences.

If we turn to the relation between stand and yield, we shall again find a strong disturbance of the normal correlation as shown in the following:

TABLE III

CORRELATION BETWEEN STAND AND YIELD

Cutting	1st	2d	3d
Correlation	+ .78 ± .04	+ .55 ± .07	+ .47 ± .08
Cutting	4th	5th	6th
Correlation	+ .54 ± .07	+ .10 ± .10	+ .70 ± .05.

The exceptionally low coefficient of the fifth cutting was due to the low yields on the part of plots which had good stands but were relatively inactive during the hot weather and partial water famine which occurred at this period. On the other hand, certain plots through their resistance to heat and consequent activity at this period, overcame to a large extent their handicap of poor stands, and nearly obliterated the usual plus correlation between stand and yield.

The data thus studied *en masse* indicate at least two physiological groups which are unequally sensitive to the climatic changes which occur in the course of a growing season, and whose reactions were sufficiently strong to change almost completely the order of the productivity of the plots. In order to test this conclusion let us turn to the individual plots and endeavor to discover and classify the physiological varieties indicated above.

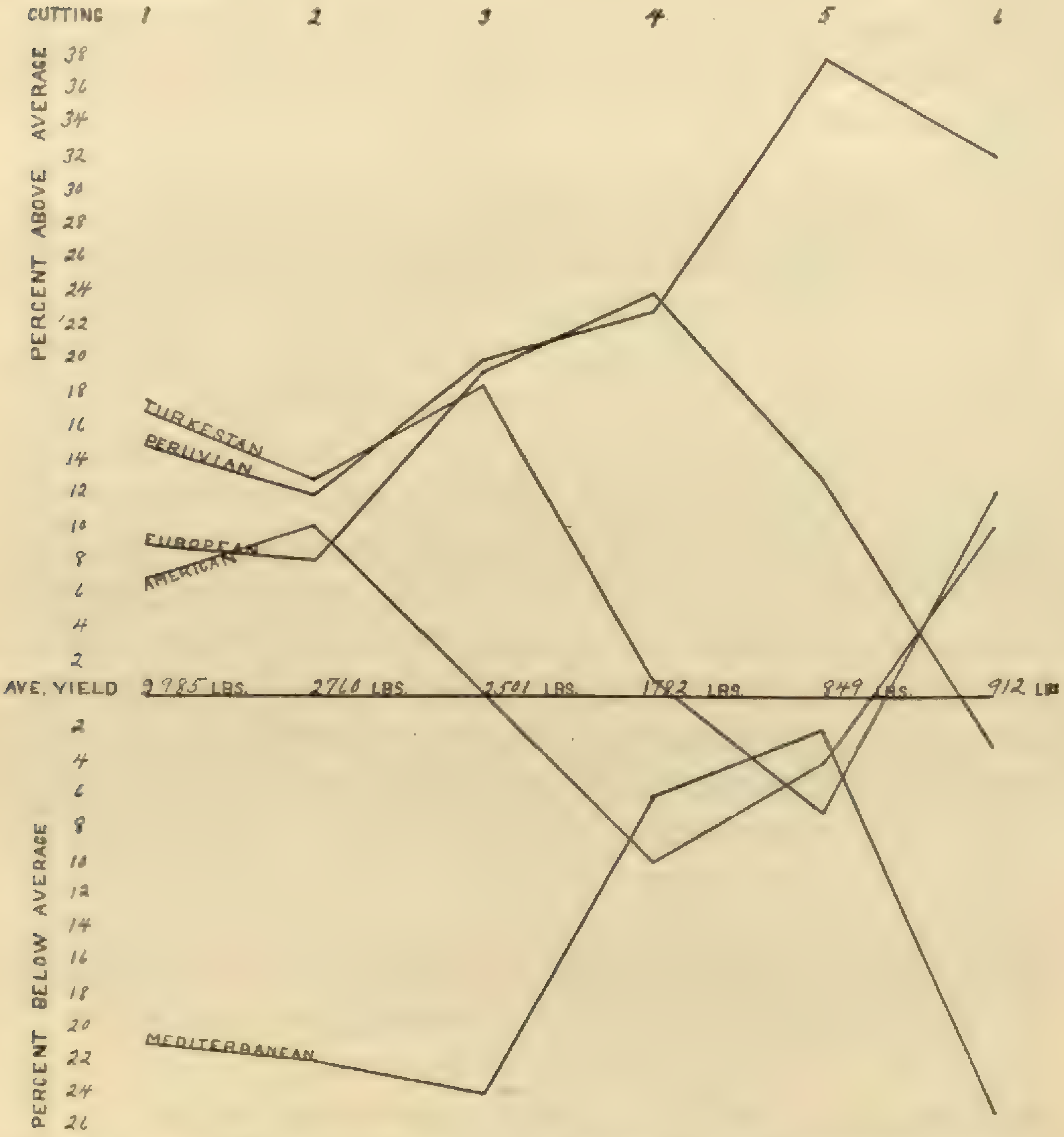
If, now, we arrange the forty-four regional strains according to their morphological characters and geographical origin, we shall have five more or less distinct groups as follows: Mediterranean, Peruvian, European, American and Turkestan. The behavior of these varietal groups through the course of six cuttings during the summer of 1910 substantiates the conclusions already drawn and illustrates the sharp differences in climatic reactions which may be observed in the several varieties of a single species.

Morphologically the Mediterranean and Peruvian alfalfas are so distinct in type that any one at all familiar with the different kinds of alfalfa would recognize them at a glance, whether a whole field or a single plant be observed. The presence of yellow or greenish blue flowers also determines a variety to be of northern origin with mixtures of falcata characters, which usually carry with them resistance to cold and drought. Otherwise, the Turkestan, American and European types are so nearly alike that only an expert would recognize them in mass culture. The individual variations within these three types intergrade to such a degree that one could scarcely assume to judge, from the observation of a single plant, the type prevailing in the field from which it originated. The three types, however, differ markedly in their physiological reactions as we shall presently see. The distinctions, in this regard, as exhibited on our plots, are not nearly so marked between the American and Turkestan alfalfas as between these two types, on the one hand, and the European, on the other. However, in northern climates where winter resistance enters as a potent factor, the Turkestan alfalfa exhibits greater hardiness than the American form, and, therefore, is able to maintain a more perfect stand through seasons of extreme frost.

When grown under Arizona conditions, the average yields of each of these five type groups present seasonal curves at once striking in their diversity and contrasts. These differences are exhibited more easily by plotting the average of all the plots as a straight line, and the average of the different groups as percentages of the total average above and below the general average line.

In observing Fig. 1, we are first impressed with a marked similarity in the performance of the European and Mediterranean alfalfas, on the one hand, and the American and Turkestan on the other, and also with the striking differences exhibited between the two groups. Although the average yield of the European plots greatly exceed that of the Mediterranean plots, the shapes of their respective

curves are almost exactly alike, the greatest relative yield of each being in the heated part of the summer after the beginning of the water famine. In like manner, the American and Turkestan varieties made similar relative yield curves, that for the Turkestan being slightly above the curve for the American strains. Here, however, the



Relative Yield of Regional Varieties Based on the Average of All Plots as 100 Per Cent.

curves bend strongly downward in mid and late summer, as if these types were much less resistant to the accumulative effects of drought and heat. In fact, it would seem that during the hot period included within the fifth cutting

(July and August), the American and Turkestan varieties were comparatively inactive, yielding only about eight hundred pounds of dry hay per acre, as against more than a ton and a half each on the first cutting. The relative yield curve for the Peruvian type stands separate and distinct from the others. Although here, as with other varieties, the yield declines with the advance of the season, the persistence and vigor with which this strain resisted the summer heat and drought caused it to gain rapidly on the other varieties in relative yield throughout the season until the very last cutting, when there was a slight decline.

Disregarding the shape of the curves we may now notice the total yield for the season. In this respect the different regional varieties take the following relative order: Peruvian, European, Turkestan, American and Mediterranean. It is here noticeable that, though the European and Mediterranean varieties have similar seasonal yield curves, they are not contiguous in the arrangement based on total yields. This is a result of a marked difference in the stand maintained by the two varieties which averaged ninety-two per cent. for the former and seventy-four per cent. for the latter. In their ability to maintain stand, the Peruvian, European, Turkestan and American varieties were about equal, averaging 92, 92, 93 and 94 per cent., respectively. The lack of stand on the part of the Mediterranean alfalfas was not due to the poor quality of the original seed, for all of these plots once had perfect stands. This behavior is also in accordance with the records of other fields of Mediterranean alfalfa in the southwest, which have come under the observation of the writer. The explanation of the weakness of the Mediterranean and corresponding strength of the otherwise similarly reacting European alfalfa in maintaining stand under Arizona conditions is a subject for further careful physiological study.

The recognition, analysis, and calibration of these differences of the physiological reactions of varieties are thus seen to become a first essential in the study of climatic adaptation, and form the basis for rational procedure in the choice of varieties and in selective breeding for the improvement of the same.

Correlations

In the improvement of varieties of plants, quality is often as important as quantity of yield. This is especially true in a forage crop, such as alfalfa. Since nitrogen, next to fat, is the most expensive of the necessary food constituents, it may be taken as the measure of quality. Commerical buyers judge alfalfa hay by its purity, odor, color and percentage of leaves retained in curing and baling. The value of the leaves lies in their relatively high nitrogen content and the consequent increased food value which they impart to the hay. Expressed quantitatively, the correlations between the nitrogen content of the hay and the percentage of leaves for the six cuttings were as follows:

TABLE IV

Correlation between Nitrogen Content of Hay and Per Cent. of Leaves

Cutting	1st	2d	3d
Correlation	+ .46 ± .08	+ .61 ± .06	+ .72 ± .05
Cutting	4th	5th	6th
Correlation	+ .68 ± .05	+ .61 ± .06	+ .52 ± .07.

That the final value of the hay is markedly dependent upon the composition as well as the percentage of leaves is shown by the following high and fairly uniform correlation between the nitrogen content of the hay and the nitrogen content of the leaves:

TABLE V

Correlation between Nitrogen Content of Hay and Nitrogen Content of Leaves

Cutting	1st	2d	3d
Correlation	+ .69 ± .05	+ .73 ± .05	+ .42 ± .08
Cutting	4th	5th	6th
Correlation	+ .67 ± .06	+ .85 ± .03	+ .74 ± .05.

If, now, we have shown that the quality of the hay depends primarily upon the percentage and composition of the leaves, we may proceed to investigate those factors which indirectly modify the feeding value by influencing the amount or character of these organs.

The factors most profoundly affecting the percentage of leaves were yield, height and stage of maturity at which the cutting was made. Local or varietal forces were

sufficiently constant to hold the place variation of this character to the plus side of the equation for four out of five determinations made, as is seen in the following table:

TABLE VI

PLACE VARIATION IN PERCENTAGE OF LEAVES

Cutting	1 and 2	2 and 3	3 and 4	4 and 5	5 and 6
Correlation.	+ 10 ± .10	+ .23 ± .10	+ .16 ± .10	+ .46 ± .08	— .12 ± .10.

These correlations, however, are low and seem to indicate that the natural varietal traits were being overcome and obscured by other variable factors.

Contrary to expectation, the stand had little to do with the percentage of leaves, as the following low and inconstant correlations show.

TABLE VII

CORRELATION BETWEEN THE PERCENTAGE OF LEAVES AND STAND

Cutting	1st	2d	3d
Correlation	— .14 ± .10	— .02 ± .10	+ .03 ± .10
Cutting	4th	5th	6th
Correlation	+ .10 ± .10	+ .07 ± .10	+ .24 ± .10.

On the other hand, the relation between height and yield and percentage of leaves was constant and marked, except in the last two cuttings.

TABLE VIII

CORRELATION BETWEEN PERCENTAGE OF LEAVES AND HEIGHT AND YIELD

Cutting	1st	2d	3d
Yield	— .41 ± .08	— .60 ± .07	— .15 ± .10
Height	— .48 ± .08	— .62 ± .06	— .68 ± .05
Cutting	4th	5th	6th
Yield	— .40 ± .09	+ .20 ± .10	+ .30 ± .09.
Height	— .55 ± .07	+ .09 ± .10	+ .19 ± .10.

The sudden change from minus to plus in these correlations should be noted. The average heights of the first four cuttings were 32, 30, 28 and 27 inches, respectively. The average height of the fifth and sixth, were 15 and 12 inches. This would suggest that at or below 15 inches the mutual shading of the stems is not sufficient to cause an appreciable shedding of the lower leaves. Up to this point, moreover, growth usually takes place by an increase

in the number of nodes, each with its accompanying leaves and side branches. Above fifteen inches, however, the principal growth in height consists in a lengthening of the internodes and, consequently, a relatively greater production of stem as compared with leaf tissue. In this physiological correlation lies the core of the difficulty in breeding at once for quality and quantity. The act of high production within itself cuts down the quality of the product by reducing the ratio between the leaves and the stems.

This difficulty, moreover, occurs in the composition as well as the percentage of the leaves. The correlation existing between the nitrogen content of the leaves and the number of days required to mature a cutting is shown in the following table:

TABLE IX

Correlation between the Nitrogen Content of Hay and the Period Required for Maturity

Cutting	1st	2d	3d
Correlation	—.33 ± .09	—.30 ± .09	—.27 ± .09
Cutting	4th	5th	6th
Correlation	—.52 ± .07	—.50 ± .08	—.17 ± .10.

Quickly maturing varieties thus have leaves richer in nitrogen than those which require a greater length of time for completion of growth. When, however, we take the average number of days required throughout the season to mature a cutting for each plot and compare this with the total seasonal yield we find a correlation of + .43. Thus we are again confronted by a minus correlation between quality and yield which must be overcome if we would make progress simultaneously in both lines.

As further examples of antagonistic correlations, a few instances may be taken from the data furnished by forty-three plots of pure races of alfalfa grown during the summer of 1910. The correlation between height and percentage of leaves was again constant and marked. The results here paralleled those found for the regional varieties. Whereas yield was uniformly correlated positively with both stooling capacity (av. No. stems per plant) and height, it is interesting to note that there was also a uni-

TABLE X

CORRELATION IN PURE RACES

Correlation Between	Cuttings			
	July	August	September	October
Green weight and average number stems	+ .75 ± .04	+ .42 ± .08	+ .62 ± .06	+ .50 ± .08
Green weight and average height	+ .01 ± .10	+ .44 ± .08	+ .22 ± .10	+ .33 ± .09
Average height and number of stems	— .29 ± .09	— .19 ± .10	— .32 ± .09	— .21 ± .10
Average height and per cent. leaves	— .39 ± .09	— .15 ± .10	— .55 ± .07	— .51 ± .08

form minus correlation existing between them. We thus have two factors both making for yield, but seemingly (probably physiologically) antagonistic to each other. In breeding for high yielding strains we are here again called upon to overcome by selection an antagonistic physiological correlation.

This brings us to the following final conclusion which the writer wishes to emphasize:

In economic plant breeding one frequently encounters physiologically negative correlations such as those, in alfalfa, between height and stooling capacity, height and percentage of leaves, and between yield and quality. In seeking improvement, therefore, the breeder must recognize and make use of these facts in the interpretation of results obtained, and also search for races which violate such naturally antagonistic correlations to the greatest possible extent.

General Conclusions

That the complex of allelomorphs, which we call a variety, may be definite as both to ultimate composition and organization is not here questioned. When, however, we consider that visible characters are only the expression of the reactions of the vital forces of the plant with the environment, we can realize that the variety, as we see it, is not a definite thing, but is a result of two independent classes of factors. Change either and the result correspondingly changes.

We are therefore to look upon the variety as a delicately organized chemical compound. The various factors of climate and soil may be compared to different physical influences to which the original compound may be subjected. As the chemist would expect reactions varying in accordance with the physical stimuli used, so will the plant react in agreement with the different environmental combinations. The extent to which this will change the nature and appearance of plants is often far reaching. Cook, working with cotton, has found that certain cultural conditions at an early stage of growth will make profound differences in the method of branching which determines the whole subsequent development of the plant and affects materially its economic value. Cultural and climatic reactions often lead to error among those who assume them to be mutative changes induced by the new conditions. That these reactions may bring to light sub-races with hereditary tendencies not hitherto called into expression and which, by selection, may be secured as pure races, is the probable explanation of many cases of supposed direct climatic adaptation.

Thus, realizing the true nature of a variety, we can draw further upon the analogy of the chemist who investigates an unknown substance by testing its reactions with a large number of known reagents. In like manner the breeder can only understand the true nature of the hereditary vital forces within a plant after he has tested and calibrated its reactions against a variety of soil and climatic factors. These reactions are of interest to the farmer only in so far as they affect the economic value of the variety as grown in his own locality but to the breeder and student of heredity their importance is fundamental. This is so because they enable him to classify, coordinate and interpret the experimental results that he obtains. This ability finally must form the basis of all rational procedure, whether one be engaged in the study of pure genetics or in the operations of practical plant improvement.

TAXONOMY AND EVOLUTION

By X.

"Some passages in this book, if taken alone and read hastily, may appear to discourage systematic Zoology. This is far from my intention. No one can study the great naturalists of the seventeenth and eighteenth centuries without feeling how seriously their work is impaired by the defective systems of the time. It is not systematic but aimless work that I deprecate—work that springs from no real curiosity in Nature and attempts to answer no scientific questions."—L. C. Miall, "Natural History of Aquatic Insects," Preface, p. i.

Introduction

Linnæus bestowing Latin names upon animals and plants was simply tripping gaily across the back of a half submerged Behemoth and mistaking it for dry land. Now the beast is careering around, and in spite of zoological congresses and international rules nobody quite knows what to do with him. No doubt when some zoological czar arises and issues his fiat a uniform system of nomenclature will be adopted and things will begin to straighten themselves out. This can only be a matter of time—the past can not be altered. On systematists to-day necessarily devolves the dull, difficult and important duty of going through the descriptive work of the early naturalists and emending it; so that Spallanzani's derisive sobriquet of "nomenclature naturalists" was a little unjust, even in his time.

Whatever opinions may be held upon the genius of Linnæus, in justice to him it should be said that it was not until his example had been followed by a crowd of other workers eager to attain to immortality by way of the back door he had left open that the fat was really in the fire.

Well knowing the confusion into which systematic work in zoology was brought by the early naturalists, modern systematists in our opinion will be the authors of a similar confusion in the future if some of the slipshod methods of modern systematics are not corrected. Moreover, a confused nomenclature is not the least of the evils which second-rate systematic work brings in its train.

Systematists with a proud curl of the lip may tell us that the work is not done now as it once was. Indeed, to those who are not able to project themselves into the future it may seem incredible that the systematists of a later date will be able to find much room for complaint in the elaborate descriptions and careful figures of modern descriptive writers. For the moment, however, it suffices us to point the parable by remarking that in 1780 Spallanzani was able to refer to the "beautiful figures" and "careful descriptions" of a systematic worker on frogs. We, of course, know without seeing them that the figures were not beautiful nor the description, careful—any way in the sense of being complete. We have therefore to reflect whether the zoologists of a future generation will find the work of to-day any freer of faults than that of the past centuries.

Systematic Work. General Considerations

It is necessary to insist at once that systematic work is not merely a question of nomenclature, names and novelties. Systematists have only themselves to thank if such a narrow conception of their province is very widely spread, especially among morphologists and anatomists, who are ready to belittle the value of the systematists' work. But science is measurement and zoology—if you like—is description, and it is impossible to dispense with the systematists' descriptive work. But we think it possible to dispense with a good deal of stuff after this fashion:

Metopidium high, suprahumerals rather long, acute, arcuate and curved at the tips. Pronotum roughly punctured at the bottom of fine furrows. Color dark-ochreous. Posterior horn uniformly cylindrical, undulating or sinuous without rugosities. Underside, scutellum and legs sordid-ochreous.

The phrase "sordid ochreous" comes ready to hand and makes it unnecessary for us to go in search of a suitable comment.

"This is the 30th memoir" writes a systematist "on the Zonitidæ which I have published in this journal, describing in all about 560 new species." We feel inclined to put our hands resolutely on his shoulders and inquire if he ever saw a ctenophor swimming in the sea or watched the progress of an *Asterias* towards its prey.

No one can look unmoved upon the Hymenopteran or Helicoid specialist with head bent over a drawer full of shells or dried insects on pins. It is not that we resent concentration or enthusiasm or even specialization, but the systematist has lost touch with his own science of zoology.

Zoology, a cornucopia of marvels, lies at his elbow full to overflowing, but he is unmindful of it. It is as if a man should use the Parthenon only as a convenient place on which to strike a match for his pipe.

The divorce between systematic work and the rest of zoology is the more regrettable because it is practically complete. It is, we admit, expedient that zoology should be divided up into anatomy, morphology and so on. But such a division is allowable only when it is expedient, while for intellectual purposes such a division is and has always been a danger. To obtain facts one must be an analyst, to consider them one must be a synthesist. Between the two there is all the difference between a hodman and a natural philosopher.

But our contention is that not even the plea of practical expediency can justify the extreme state of specialization into which systematic zoology has fallen, making itself manifest in the concatenation of such purely artificial characters as that "the third joint of the antenna is longer than the second, that the mesoscutellum is ovate and the color pink with blue spots." All this simply makes one yawn, though there is this much to be said in favor of this stamp of systematist, that nothing bores him so much as the recitation of one of his own diagnoses or being introduced to the systematist of another group.

Systematic work is a withered branch of the biological tree which there is still hope of rejuvenating. Treviranus long ago remarked that if we once regarded systematic work as a part of biology and nomenclature as a means to an end rather than as an end in itself, both might take their places in science. Let us take every precaution against systematic work becoming one of those unproductive and artificial pursuits which spring up like mushrooms around centers of splendid endeavor and high achievement. After Shakespeare came his commentators. Shall it be said that after biology came the systematists?

We assume that the principal object of systematic work is to discover the *phylo-genetic classification* of animals, for which it is surely necessary that every animal as it passes through the

systematists' hands should be, as far as possible, thoroughly examined and described, no dependence being placed upon a few superficial characters usually selected from the external parts? That the systematist should concern himself, as he does, with the external parts, leaving the anatomy to other workers, we consider is as bad for the systematist himself as it is bad for the science; for himself, he is doing work which can only keep his soul alive with difficulty—superficial clerical work which can be "prompted by no real curiosity and attempts to answer no scientific questions," and the results of the work itself is often invalidated by the arrival of the destroying angel in the person of the anatomist. For a superficial description often means a wrong classification; whence it follows that any zoo-geographical deductions therefrom are invalidated; while a careless description usually ignores the possibilities of variation and shows no evidence of pains having been taken to make identification easy.

Systematic work, then, is concerned with classification, geographical distribution, variation and identification, and there would be no need for this paper, if it were more generally realized that one thorough examination and description of the whole animal assists those branches of the inquiry more than twenty loose and superficial ones.

Of course systematic workers are not the only zoologists who over-publish; yet they especially might cultivate a little of the salutary reticence of C. L. Nitsch and Alfred Newton, who, with no discredit to themselves, wrote and published little, yet it must be admitted by those with an eye on the extravagant output of others, to the advantage of zoology. The words "res non-verba" were the motto of Delle Chiaje, who, like Nitzsch, on his death left behind many important discoveries unpublished and only indicated in his drawings.

Classification in General

The coming of Evolution meant for systematic workers that no system of classification would henceforth be considered as a serious contribution to science, which was not constructed on phylogenetic lines. It meant the final overthrow of such ideas as Agassiz held, that the divisions of the animal kingdom were instituted by the Divine Intelligence as categories of his mode of thought—of such fantastic systems as those of Rafinesque and Swainson and such strictly artificial ones as the arbitrary ar-

rangements of convenience which should be now used only in those groups where, and for as long as, our knowledge of the anatomy is so slight that some sort of temporary device for sorting out genera and species has to be adopted.

The ideal system is now phylogenetic, *i. e.*, it aims at reconstructing in a genealogical tree the actual lines of descent.

Only those who have attempted the reconstruction of phylogenetic trees understand the intrinsic difficulties of the work. There can be no doubt that the coming of Evolution has put before the systematist a very difficult task. As to whether the methods usually employed by him are adequate to the demands placed upon them we are frankly sceptical.

Fortunately for the systematist the main lines of classification in most groups are given him ready made by the morphologists who have laid down the foundations trusting to the "systematist" to fill in the details. Such classifications—the main phyla, classes and orders are of permanent value, because they are founded upon a combination of characters of tried worth judiciously selected after a careful survey of extensive embryological and anatomical data.

Single Character Classification

On the other hand the minor systems—the families, genera and species—the realm of the "systematist"—too frequently consist of haphazard combination of a few characters selected because of their convenience in not entailing any anatomical work, or selected on account of the ignorance existing of any other—particularly internal—important characters. Ignorance of their morphology has been the main reason for the difficulty in classifying the Coleoptera. Entomologists are especially prone to give their whole attention to what is visible without the aid of dissection. In the Polyzoa the majority of forms are only known by their external appearance and their classification is proportionally unsatisfactory. In the Mollusca reliance is placed on the shell; in mammals the skull and the skin, in birds the plumage are the articles of faith.

Single character classification or diagnosis by one or two characters, as zoological history shows, has proved inadequate—that it is unphilosophical is patent to all.

Such single character classification even when practised by

the great morphologists, men who, being acquainted with the whole of the anatomy of the forms they were classifying, deliberately selected one or two characters after a survey of the whole—was rarely a success. Huxley set out unabashed to classify birds by their palate, and Agassiz fish by their scales—systems which have now shared the fate of most others which set out to erect a classification on the modifications of a single organ alone. Alfred Newton said that there was no part of a bird's organization that by a proper study would not help to settle the great question of its affinities.

The systematist who deals with the minor subdivisions of the animal kingdom—families and genera—should be as much a morphologist as the one who deals with the larger—the phyla and classes.

Description

We have pointed out above that the adequacy of a system of classification depends in great measure upon the thoroughness of the description of the species and genera. Classification in all groups has progressed in just proportion to the more exact examination of the species considered in the classification.

The history of zoological research brings out this fact very clearly, beginning with the work of Linnæus, the originator of the superficial diagnosis, passing on through Cuvier, who appreciated the value of anatomical knowledge, to Von Baer, who emphasized the importance of embryology.

It was not a "systematist" as we know him who first correctly classified *Lepas*—the conchologists blindly accepted it as a Mollusc. It was not a "systematist" who first established *Peripatus* as an Arthropod, for the first describer of that animal regarded it as a slug!

How rare it is to find in a description of a new species anything more than an indication of the external parts. It is a peculiarly arbitrary limit to a man's curiosity that restricts his enquiry to the superficial aspect of an animal. A natural philosopher ought never to be satisfied with the external appearance of things. The wisdom of the ancients bids us "beware of what things appear"; and the method of our modern science is one of close and detailed observations. In scattering names broadcast with liberal largesse upon species, varieties and

genera, systematists have sometimes dropped into some curious errors. Teratological specimens have been described as new species and most zoologists have heard of the man who described as a new species the longicorn beetle, the head of which having fallen off, had been fixed on upside down. His examination of a new species makes so slight an impression on his mind that sometimes the same worker has described the same form twice under different names.

The descriptive papers on Mollusca usually consist of short descriptions of the shells, even written in a dead language. This is conchology. Conchologists confine themselves to the patterns and shapes of shells—nature's medallions—numismatics! Much of this work—along with similar productions in entomology and carcinology—we regard as positively flagitious.

Sir Ray Lankester in the article "Zoology" in the Encyclopædia Britannica (ed. XI.) remarks that museum naturalists must give attention to the inside as well as to the outside of animals and that to-day no one considers a study of an animal's form of any value which does not include internal structure, histology and embryology in its scope. Agassiz, too in his famous "Essay on classification" wrote that "the mere indication of a species is a poor addition to our knowledge when compared with such monographs as Lyonnet's *Cossus,* Bojanus' 'Turtle' Strauss Durckheim's *Melolontha* and Owen's *Nautilus.*"

"But," it will immediately be asked in chorus, "do you seriously suggest that a monographic volume should be devoted to every new species?"

This is a leading question which brings us to the crux of the whole matter, and can not be answered in simple "Yea" or "Nay."

The Provisional Diagnosis

The amount of analytical study that may be given to any one animal form in any one stage of its development is infinite. The result is that in describing a new species for the purposes of exact phylogenetic classification there must be a limit beyond which it is unnecessary to go. Such a limit can not be otherwise than arbitrarily selected according to the best judgment of the systematic worker as to how much analysis is required to place his new species, although at present, *miserabile dictu,* relatively

very few animals have been thoroughly explored, yet in the distant future, in the millennium, it can not be doubted that every genus, even every species will have been examined *in toto* in every stage of its development and life-history as thoroughly as our instruments and eyesight will allow, and perhaps a whole volume or several volumes will be devoted to every animal form. At present, however, it is a waste of ink to consider a future so far away. A more pressing duty is to consider how far modern methods of superficial diagnosis fulfil the obligations placed upon systematists not to give an exhaustive analysis of animal forms, but to give sufficient data to meet the searching demands of phylogenetic classification.

We are aware of the fact that the convinced and determined systematist does not maintain that the method of superficial diagnosis does meet or is intended to meet the demands we have been indicating. If he reads as far as this and does not throw aside this paper in contempt, he is ready with eager forefinger and glib apology to convict us of begging the question that systematic zoology can be ever anything, or should be ever anything more than we have said.

It is often argued that the superficial diagnosis of the systematic worker is simply a provisional diagnosis awaiting the confirmation of the anatomist. A plausible defence of the provisional diagnosis is advanced by many workers in perfect good faith which it is now necessary to anticipate and examine.

This argument defends the provisional diagnosis on two grounds: (1) The advertisement theory; (2) the recognition mark theory.

The supporters of these theories admit that the provisional diagnosis in no way settles either an animal's systematic position or its validity as a species. But it is alleged to be of value and should be encouraged because it advertises the existence of a presumptive new form which would otherwise remain unknown and overlooked in the store rooms of the museum and laboratory, and because in giving an account of the external parts, at all events, the systematist is describing those features by which we are more or less easily able by a superficial examination to recognize summarily the form when it turns up again.

The first part of our answer amounts to a recapitulation of what has been previously stated in general, viz., that systematics have lost touch with the rest of the science. The output of systematic

work and the output of anatomical and morphological work nowadays move along completely different channels. The work turned out by the systematic worker is scarcely, if ever, conceived in the light of modern biological theory, is rarely couched in terms of modern biology and rarely indicates a problem to be solved or a question to be answered. It proposes distinctions the anatomist sweeps away and hazards affinities the morphologist laughs at. It performs work that has to be done over again, and instead of giving the morphologist what it claims to give him—a sketch map of the country he is to traverse—all it does is to bewilder him with a Will-of-the-Wisp's lantern, an intolerable multitude of slipshod and untrustworthy directions that he has come instinctively to suspect. We can not too often ask the question, why should the work be done twice? Surely it is time that something were done to stop this tremendous rush for publishing provisional diagnoses that more time could be devoted to the systematic study of animal forms, obtaining thereby sound phylogenetic classification, sound deductions in geographical distribution, valid species and a less confused nomenclature.

Thus the systematist's protest that at least he "advertises" presumptive new forms we can reply that he may do so, but that for any purpose other than a dull census of the animal kingdom with a very generous "±" to it, he is a positive Benedick of zoologists, for "nobody marks him."

The upholders of the provisional diagnosis will say that at any rate they are giving us a description of the external parts and are increasing our knowledge by so much. True, but by so inconsiderable an amount that when the anatomist comes along with his scalpel he so quickly disposes of the external parts merely by the use of his eyes that it is a matter of indifference whether the former have been described or not. Moreover, the great majority of the tens of thousands of descriptions that are issuing from the press are of animals so closely related to previously described species that such descriptions really amount to little more than a recitation of their distinguishing characters.

It is certainly useful to know that *Caccabis rufa* is to be distinguished from *Perdix cinerea* by its red legs and that the Leporidæ can be discriminated by the character of their upper incisors. But the question may well be asked, what is the use of being able to distinguish one species from another without

being able to record at the same time anything about its bionomics or anatomy which would give the distinction its real value. A great deal is known about the partridges and hares, hence the distinctions alluded to above are useful as an easy way of quickly identifying them. But so long as nothing is known about either of two species that are distinguished we are none the worse off, if both remain indistinguishable.

Finally we would point out that of all people the systematist should know that at present of the forms he advertises and describes so copiously and summarily only a fractional part is, or can be, dealt with by the laboratory worker. We are speaking now of the anatomy pure and simple of new species and genera. The laboratory worker proceeds slowly, is fewer in numbers and has other problems—embryology (descriptive and experimental), heredity, physiology (descriptive and experimental) and morphology to attend to besides purely descriptive anatomy. And yet anatomy—the very corner stone of the temple of zoology—has to be restricted in output because none of the systematists will learn how to use a scalpel or look down a dissecting-microscope—feats in themselves perfectly easy and calling for no special training or faculties.

Possibly the upholders of the provisional diagnosis will maintain that by publishing his account of the difference between closely allied forms the systematist is providing the biologist with a stimulus to discover how much deeper such differences go. But surely it is a strange perversion of a man's natural instinct of curiosity that enables the systematist to rest content with advertising problems instead of endeavoring to equip himself for the task of undertaking them himself, who is eminently suited to the work and whose occupation daily brings him into close contact with them.

Finally we would point out that the enormous mass of species which have been created upon superficial diagnosis so far have remained unincorporated for the most part in the structure it is designed to build up, viz., a clear comprehension of the phylogeny of the lesser divisions of the animal kingdom. It is as though a man were to set about building a house by making a vast quantity of bad bricks and then to leave them scattered about his site in the hopes that some one would come along and make a house of them. Surely it is an economy of effort for the systematist to take up the bricks and build himself, what time

the embryologist and morphologist are engaged upon their own special tasks.

The Comparative Value of Internal and External Parts

Briefly reviewing the discussion as far as we have carried it, it will be seen that we are asking for sound phylogenetic classification of the smaller groups as well as of the larger ones, based not upon single characters, but upon the whole of the characters regarded collectively, for more careful and more thorough morphological methods in description and for the discontinuation of the provisional diagnosis. In view of the desirability of working up sounder schemes of classification from the enormous, unwieldy and superficially known mass of genera and species systematists can be rendering little service by continuing to turn out indiscriminate provisional diagnoses.

It remains now to discuss in greater detail the proposal we bring forward in the place of the provisional diagnosis.

The commonly accepted opinion is that while for the classification of families and orders the internal parts must be taken into consideration, for that of species and genera a summary of the external parts is all that is required. On account of the labor and difficulty sometimes involved in dissection we are too ready to assume that the internal parts in genera and species present a dismal monotomy of character which it would be profitless to investigate for systematic purposes.

If it is admitted that internal characters are of value among the higher divisions of the animal kingdom, can the systematist tell us at what precise point in the downward scale they cease to have value, and at which reference need only be made to the external parts? Even supposing for a moment that there is such a limit, we are strongly of opinion that it does not come before the genera.

A genus is of different value in different groups but as a rule it presents so much difference in external form from other genera as to warrant the inference that internal differences of a like extent will be found if sought for. At the present moment a genus is a perfectly arbitrary collection of species. We venture to prophesy that with more elaborate descriptions intergeneric relationships will be more carefully defined and genera will become less heterogeneous and more natural. But this is by the way.

A priori it seems improbable that less variety will be found among the various internal systems of organs than in the integumentary or exoskeletal parts. But an argument may be put forward that the external parts in immediate contact with the environmental forces would be the first to register change in the modification of a species. The internal parts as stanchions and bulwarks remain firm to give characters to orders and families, while change makes assault without and gives characters for species. For example, among the Asteroids it is said that the internal organization is so uniform that the only method of classification is to take the different ways in which the demands of the external environment have been met.

But generally speaking a species depends for its survival not simply upon the external front it presents to its environment. An animal's form cannot arbitrarily be divided into external and internal parts. It is an integral whole, and variation and selection may occur anywhere, while the correlation of variation is a text-book commonplace. As opposed to correlative variation there is the law of the independent variation of parts. Not only may variation occurring in one part cause a variation to take place in another, but variation may take place independently in some areas and be limited in another, so that in deciding upon the comparative value of the internal and external parts in any group consideration must be given to both these laws. In the Asteroids, we assume that anatomists have taken the matter in hand and found that the external parts vary as a rule independently of the internal which remain constant. But in how few groups has such a precaution been taken! Is it not rather the general rule simply to *assume* that the internal parts lack variation and are of no value systematically, as, for instance, in the Lepidoptera, where the Lepidopterists expect that a classification based upon the wing-markings or upon wing-neuration can express the true relationship of the various units?

Even in those groups where systematists have dissected and found the internal parts valueless it still remains necessary, in view of the law of independent and unexpected variation of parts for them, to apply the scalpel to every new form.

It is impossible to deny that the external parts are often of extreme systematic importance—they are exposed to the light and develop color patterns (although color is usually an unsafe guide if taken alone), and the external parts of such forms as

Arthropods and Molluscs being hard provide systematists with a sculpture on which it is easy to detect minute differences in pattern. On the other hand we would remind the conchologist that the external parts are by their very positions most liable to exhibit lesions and weathering, and certainly in the case of Mollusca where the dependence of the exoskeleton upon a specific article of diet (viz., lime salts) is very close, to register "fluctuating variation" according to the constitution of the medium or of the food ingested.

But here again if a more common practise were made in dissecting by systematists, variations would be found even in closely allied species making the descriptions complete and often even necessitating the erection of new genera. One of the writers was dissecting an ordinary species when he discovered that the epipharynx was so entirely different in form and structure from the usual type for the genus that, had it been an external character it would long ago have been formed into a new genus.

Karel Thon[1] has demonstrated how in *Holothyridæ* a single internal structure is at variance with the other indications of genetic affinity. A great many similar instances will be immediately called to mind by those who practise dissection.

Again, if systematists are convinced of the taxonomic value of hard parts how comes it that they need to be reminded that there are hard parts in the internal anatomy as well which they so frequently and habitually leave unnoticed? The endoskeleton of Arthropods, gastric mills, pharyngeal ossicles and cartilaginous supports are all systems which might be profitably studied by the entomologist and carcinologist, while the conchologist generally proceeds as though the radula and jaw were part of the "mush," as he so inelegantly terms the viscera.

Geographical Distribution

The advent of the morphologist into the particular sphere of systematics or the metamorphosis of the systematist into a morphologist (it matters not how we put this desirable event) will result in the annexation not only of classification, but also of questions of geographical distribution by anatomy and morphology. How many pretty theories in geographical distribution

[1] *Zool. Iahb.*, Bd. XXIII, Syst., pp. 720-21.

have collapsed because they were built on the sands of an incorrect classification? The similarity between the faunas of South America and Madagascar is supported by many facts, but the value of *Solenodon* in Cuba and *Centetes* in Madagascar has been lessened by the recognition that the two genera resemble each other by convergence, and should now be classified in different families.

The Dendrobatinæ also are considered by Dr. Gadow as an unnatural group, the two divisions—South American and Mascarene—having, according to him, lost their teeth independently. Again, Dr. Gadow refers to the Ratitæ as a heterogeneous assemblage of birds which is "absolutely worthless" for the zoogeographer. There are scores of such artificial groupings—the work of the systematist—which have led zoogeographers astray.

The result is that systematic work as at present pursued is of very little use to us in the study of geographical distribution. It is hopeless nowadays for a zoologist to sit down with a list of species and their range and trusting implicitly in systematic work to make maps of distribution and, as he so often does, to draw deductions therefrom, for the validity of such deductions must ultimately depend upon the anatomical and morphological data. Moreover the study of geographical distribution is developing new methods of tackling its problems.

We do not consider it necessary to touch on the other remedies that might be applied with a view to redeeming zoological taxonomy from its present artificial state and to bringing it into line with the rest of biology.

Such remedies—for instance, testing the validity of species by genetic experiment and the intensive study of variation—have been advocated many times before,[2] although with little success. We believe, however, that the reforms in descriptive zoology we have advocated above are the more urgent.

[2] Cf. E. B. Poulton, "Essays on Evolution," 2. "What is a Species?" and K. Jordan, "Novitates Zoologicæ," 3, 1896.

SHORTER ARTICLES AND DISCUSSION

NABOURS'S GRASSHOPPERS, MULTIPLE ALLELOMORPHISM, LINKAGE AND MISLEADING TERMINOLOGIES IN GENETICS

In a review of Nabours's breeding experiments with grasshoppers,[1] Mr. Dexter makes a distinction between an interpretation of Nabours's and his own, where I fail to see a difference except in terminology. This is so typical of much recent Mendelian work that I am tempted to call attention to it.

Nabours describes a cross between a female with characters *BI* and a male with characters *CE* and comments on the production of an individual with characters *BEI*. He says, as quoted, that the "female parent gave at least one gamete containing the factors for the patterns of both her parents (*B* and *I*) and that this double character gamete was fertilized by one of the *E* gametes which came from the *CE* male."

Dexter prefers to call the supposed exceptional *BI* gamete of Nabours *BceI*, and the supposed *E* sperm which fertilized it *bcEi*, stating that Nabours's terminology would involve multiple allelomorphism, his own linkage. (Nabours uses, I think, neither expression.) Now what is the difference between the two interpretations? Is it anything but verbal? Is there anything significant in the small letters which Dexter has added to Nabours's formulæ? If so, what is their significance? Do they mean any more than the extra zeros in the expression 1.000 as compared with 1.0?

Dexter proposes an experimental test, that the cross be repeated. "If then *BEI* forms should appear again and in these when mated to other forms the factors *B* and *I* should be found to stay together to the same extent as they before separated, it would show that close linkage, rather than multiple allelomorphism explains this particular instance." How would it show it? If we take Nabours's assumption that *B* and *I* have exceptionally gone into a single gamete and formed with *E* a zygote *BI.E*, would it be counter to his assumption that they should subsequently hang together and that gametes should arise *BI* and *E*, respectively? Would adding a few small letters to the formulæ

[1] Am. Nat., May, 1914.

alter the case, changing it from multiple allelomorphism to linkage? It seems to me that this is one more case in which a fallacious conclusion is reached in consequence of using small letters for *absent* characters in Mendelian formulæ. Professor James Wilson has pointed out others.

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BUSSEY INSTITUTION,
FOREST HILLS, MASS.,
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PATTERN DEVELOPMENT IN MAMMALS AND BIRDS

GLOVER M. ALLEN,

BOSTON SOCIETY OF NATURAL HISTORY

THE particular coloring of mammals and birds is produced by two factors—pigmentation and the physical structure of the hair or feathers. Both are often present together. In certain mammals, for example the golden mole (*Chrysochloris*) and the European Galemys, a beautifully iridescent sheen is produced by the reflection of light rays having a certain angle of incidence upon the hairs which themselves contain pigment of a characteristic color. In the duckbill (*Ornithorhynchus*) the same thing is found. The peculiarity of feather structure that causes iridescence is largely developed in certain families of birds, as the hummingbirds and the pigeons (see Strong, 1904, for an account of the feather structure).

It is not my purpose to discuss the *use* of this iridescence to the bird, beyond stating my belief that it is in part at least for sexual display, as no one can doubt who watches the male street pigeon strutting before his mate. With amorous coos and lowered head, he confronts her and, swelling out his throat feathers, turns about and about, so that the light is reflected from his neck and throat in a sparkle of rainbow hues. It has also been suggested (Thayer, 1909) that iridescence may be a strong factor in concealment, since from the variety of the colors produced the bird is more difficult to resolve from its many tinted environment amid foliage and flowers.

With many birds the characteristic coloration may not be at all that of its pigment. Thus the blue of the male indigo bird (*Passerina cyanea*) is due solely to the physical structure of its feathers which though pigmented with brown, appear blue by reflected light. If, however, a blue feather be immersed in oil and viewed under a microscope by *transmitted* light, it is seen to be *brown*-pigmented. The physical feather-structure of the adult male is thus in this species a secondary sexual character chiefly developed during the breeding period.

The important point at present is, however, that the color effects just described are none the less due to pigment, quite apart from the fact that the apparent color of the pigmented area may be different from the actual color of the pigment (except that iridescence may sometimes be faintly seen in an unpigmented feather).

The use of pigmentation to its possessor is a matter still under discussion and investigation. In many cases it is doubtless the result of purely physical causes and it is quite without the power of the animal to make use of its coloration for outward effect. Thus the beautiful colors inside the shells of some molluscs are never apparent from an exterior view, and are supposed by some to be in part a waste product, the result of metabolism within the organism.

The present discussion has to do only with the external pigmentation of the hair and feathers, respectively, in mammals and birds.

The simplest cases of coloration are those in which the body or its covering is everywhere of the same hue, or nearly so—as in the elephant, the wild buffalo, or the house mouse in which the hairy covering (or hide in the elephant) is of a nearly uniform tone everywhere. So too, the crow, the apteryx, and the nestlings of many birds whose parents show a more highly differentiated style of markings. Such mammals and birds, so far as the development of pattern is concerned, I would consider unspecialized, yet it does not follow that in this

respect they are also primitive, though in most cases I venture to think this may be true. The uniformity of plumage is probably a derived condition in such a species as the Cuban blackbird (*Holoquiscalus assimilis*) in which the duller colored females have yet a yellow patch at the bend of the wing, a style of marking widespread among allied forms. The adult males, however, have lost this and are wholly black. Gadow as well as Keeler (1893) conclude that among related species in which there is a tendency to differentiation of the coloring the end result of the stages through which the species may pass is the production of a wholly black bird. In general a wholly black condition is no doubt to be considered as a derived rather than a primitive state among birds whereas a uniformly dull plumage of a brownish or grayish tone is probably in most cases primitive. Among mammals the same is probably also true, for in both the black condition indicates either an excessive production of the black over other associated pigments, or a loss of the power to produce the latter, whereas the neutral gray or brownish coloring is due to a more even mixture of such pigments.

As pointed out by Professor W. E. Castle, the "ticked" pattern of the hairs of mammals is probably primitive, and it is certainly very widespread. It is well illustrated, for example, by the house mouse (*Mus musculus*) or the wild guinea-pig (*Cavia*), in which three separate pigments occur as granules in the individual hairs—yellow, chocolate, and black. These three in their normal mixture produce a neutral gray tint—mouse color—and an examination of this type of coat usually shows that some hairs are wholly black, others dark at base barred with black and yellowish near the tip.

There are two ways in which patterns may be developed from a uniformly tinted covering of hair or feathers: (1) by a local change in the relation of the associated pigments so that in certain areas only one or two sorts are produced instead of three, or only one; (2) by a failure to

develop pigment at all in certain places, so that a white or unpigmented area is produced.

It is not rare among mammals to find that one or more of the characteristic sorts of pigments are not produced in certain individuals and probably the factor or factors for these are lost altogether from the somatic and sex cells alike. Such variations may be perpetuated through inbreeding and so no doubt have arisen sundry domestic color varieties of animals and plants. For example, in the course of experiments with color varieties of the house mouse (carried on some years since with Professor W. E. Castle) we found that the chocolate-colored mice which we bred as extracted recessives from black mice, contained only chocolate pigment in their hair, whereas in the black parents both black and chocolate pigments were present, but the black masked a chocolate pigment. Moreover, the chocolate mice always bred true to that color, but if bred back to the black parents, gave black young or both black and chocolate in Mendelian proportions, according to the nature of the matings. The interesting point here is that the chocolate mouse once produced, through the loss of its black-and-gray-pigment-potentiality, can transmit no other pigment character but the chocolate. What causes the occasional production of an individual in which one or more of the characteristic sorts of pigment is absolutely lacking is still unexplained. Nevertheless it is of frequent occurrence not only among domesticated species, in which the natural conditions of life are so greatly modified, but also in species in a state of nature.

A skunk normally marked, but chocolate instead of black, a raccoon likewise of normal pattern but the pigmented areas yellow, are merely examples of the dropping out of the factor for black pigment from the normal combination of the two. Such specimens are of occasional occurrence, and examples are in the museum of the Boston Society of Natural History. Similarly are produced red woodchucks or muskrats, or wholly yellow field

mice (*Microtus*). Melanism commonly results through an excess of black pigment which may mask a second pigment. Thus the black hairs of the black variety of fancy mouse commonly contain a considerable amount of chocolate pigment as well, and so of the hairs of the black-appearing skunk. A black mouse thus does not contain the yellow pigment, while the chocolate pigment is largely masked in general view by the black. In other cases it may be that black pigment alone is present.

It is probable that many cases of dichromatism among animals are explicable as similar cases in which one or other of the pigments normally present becomes to a greater or less degree inactive. Thus red forms of certain blackish or dull-colored bats (*e. g.*, the small *Molossus* of Cuba) are apparently the result of the dropping out of the factor for black pigment or its great reduction. The red and gray phases of the screech owl (*Otus asio*) are probably also explicable as a similar phenomenon.

It is only when this inactivity of one or more of the pigment factors occurs locally on the body that a definite color pattern is produced, in which neighboring areas of the body are of contrasting hues. As an example may be cited the variegated guinea-pigs, whose monotone ancestors are still abundant in a wild state in South America. Professor Castle, through his studies of these patterns in guinea-pigs, first suggested to me in 1903 that there were definite areas of the body which, though contiguous, are independent of each other in their pigment-producing capacity. In this suggestion lies the key to the chief investigation of this paper, namely, the defining of these areas, and a study of their behavior in the development of pattern by the second of the two methods previously given—that is, through the failure of pigment to develop, so that white or colorless areas result. This condition of partial albinism is not uncommon among animals which in their normal condition are completely pigmented. In domestic species it is very general and in them tends to be preserved. It also occurs normally in the shape of defi-

nite white markings in the patterns of many mammals and birds. Magazines of natural history abound with instances of total or of partial albinism among mammals and birds, either of domesticated or of wild species. Some writers have even recognized the fact that such white markings tend to occur in certain parts of the body, as at the tip of the tail or on the forehead. Darwin speaks of the white forehead spot or star, and the white feet so common among horses, and implies that such markings must be of some significance. His statement on hearsay that white-marked horses are more susceptible to poisoning from noxious herbs is, however, uncorroborated. In 1882, W. H. Brewer gathered a number of statistics as to the presence of white marks in horses and cows, but reached no conclusion. He could find no necessary correlation between the presence or absence of white spots in forehead and feet, though it appeared that white marks might be more frequent on one side of the body than the other. But the tentative conclusion that such animals habitually reclined on the side showing the more white, is begging the question.

As briefly stated in my paper of 1904, the important thing is not that white tends to appear at certain places, but the converse, that pigment production is more intense at certain definite centers on the body and the occurrence of white or pigmentless areas is due to the restriction of pigment formation at the periphery of these centers, so that white occurs at their extremities or as breaks between contiguous color patches.

In mammals and birds these centers are typically five on each side of the body, and a median one on the forehead. They appear to be homologous in both groups, though in different species they show varying degrees of modification in their behavior and development. When a reduction of the pigment areas occurs, the appearance is as it were a shrinking of the particular color patch toward its definite center. The reduction may vary to any degree, from that condition in which the break

between two adjacent patches is merely indicated by a white streak to that in which it is reduced to a small spot of pigment, or to zero, when the entire patch drops out, leaving a white area. These patches are wholly independent of each other in the extent to which they may be developed, so that a particular patch may be quite wanting on one side of the body, while its fellow of the opposite side is completely developed. Nevertheless, there is often a marked tendency to bilateral symmetry in such reduction. From a study of partial albinos in which the pigment reduction is considerable, the location of the ultimate centers of these patches becomes possible as well as the determination of their normal extent. I have studied several domesticated species in which white marks are common, with the results briefly detailed below.

When all the centers are fully developed the animal is completely pigmented; when none is developed, it is a total albino. Between these extremes may be found every conceivable degree of development. In an ideal case in which each center is slightly reduced so as to be circumscribed by white, the animal would have a dark coronal or crown patch and a series of five patches on each side separated by a median dorsal and a median ventral stripe. The anteriormost of the lateral patches center at the base of each ear, and each in its greatest development covers the side of the head from muzzle to behind the ear. These I have called the aural or ear patches; the next posterior are the two neck or nuchal patches each of which pigments its proper side of the neck, and extends from behind the ear to the shoulder and anterior edge of the foreleg. When much reduced the patch, as it were, contracts to a small area on each side of the neck, varying slightly in its location among different species. Posterior to these come the scapular or shoulder patches one on each side of the body. Each pigments the shoulder area and foreleg, except (usually) the front edge of the upper part of that member. This patch shows interesting slight variations in the extent over which it spreads in different

species. Centering nearly at the lower part of the back are the pleural or side patches, each of which pigments the area from the shoulder to the lumbar region and anterior part of the hind leg of either side. Last of all, the two sacral or rump patches, each of which on its respective side pigments the buttocks and tail. In most species these two patches are so closely associated that they tend to remain fused dorsomedially, so as to give the appearance, when reduced, of a single median patch at the base of the tail. Their frequent bilaterality, however, indicates the dual origin of such median patches. Each of the lateral patches in its complete development extends from the mid-dorsal to the mid-ventral line or those of opposite sides may overlap slightly. Reduction usually first appears mid-ventrally.

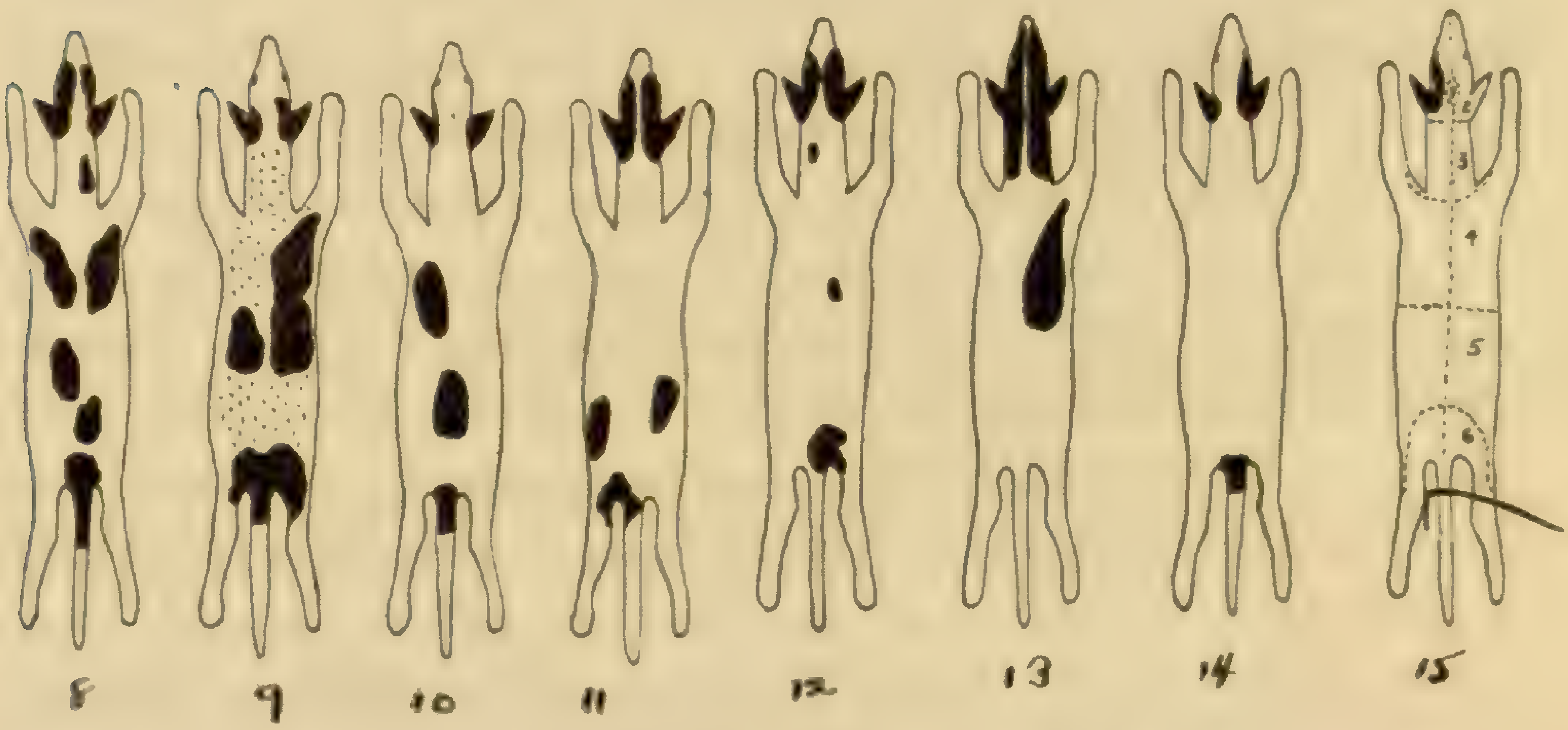
It is probable that the retinas should also be considered as an additional pair of patches, since morphologically the eye is of dermal origin, and there is sometimes seen a tendency to the formation of a small circumorbital patch, which appears to break from the ear patch when this is largely reduced.

Pocock (1907) has pointed out that in black-and-tan dogs the tan appears about the muzzle, along the sides and on the limbs, while the blacker portions are more dorsal. It may be added that in tricolor hounds, in which the several primary patches are reduced, these are often tan color at their several peripheries and black centrally. In both cases, the explanation is simply that pigment formation is less intense the farther away from the primary centers.

The reason of the division of the body surface into these independent areas of pigmentation does not here concern me. It is no doubt the result of physiological causes, and it is rather suggestive that the several patches correspond externally to important nerve centers or groups of nerves. Thus the eye pigment corresponds to the optic nerve, the aural patch to the auditory nerve, so that these two great external sense organs of the head have each their corresponding pigment patch. The neck

patch corresponds with the group of cervical nerves, the shoulder patch with the brachial plexus, the side patch with the nerves of the trunk, and the rump patch with the sacral plexus. It may be further suggested that the median crown patch of the head corresponds to the pineal eye, a suggestion that is strengthened by the fact that it is more or less obsolete in mammals, just as the pineal gland is vestigial, whereas in birds, which are more reptilian in structure, the patch is usually well defined. At all events it is a median unpaired structure, as are the pineal and the interparietal bone.

Turning now to a more detailed consideration of these pigment patches in sundry species of animals, we may first examine a series of diagrams (Figs. 1–15) of the



FIGS. 1–7. DIAGRAMS ILLUSTRATING PIGMENTATION IN THE DOMESTIC DOG.
FIGS. 8–15. DIAGRAMS ILLUSTRATING PIGMENTATION IN THE DOMESTIC DOG.

domestic dog, all of which are carefully drawn from photographs or from living animals, and are selected from a great number to show various conditions in the reduction of the pigment patches. In these and the other diagrams the black portions represent pigmented areas, irrespective of the actual colors.

For convenience I have called the white stripes demarking these chief or primary patches, "primary breaks," since they are the first indications of a decrease in pigmentation such that two adjoining patches no longer meet. Secondary or further breaks result in a general disintegration of these primary pigment patches, and are apparently more irregular in nature, though often they follow certain fairly well defined lines. The first of the primary breaks generally occur as white patches on the chest or belly, about in the median line. These are not shown in the dagrams, but in most cases should be understood as present. In Fig. 1 the pigment areas show a beginning in reduction. The two aural patches have become separated and their failure to spread to the normal limit in the median line has resulted in a white nose stripe. A short transverse white marking indicates a separation of the neck patch at its anterior edge from the ear patch. Elsewhere the various patches are contiguous; but the extremities of the limbs and tail are pigmentless, as if pigment had failed to spread to the tips of these members in its reduction. In Fig. 2 the same primary break between the ear patches is present, and in dogs it is one of the first and most frequent to appear. The same shrinkage of pigment from the extremities is also seen. The neck patch of the left-hand side, however, has completely dropped out, and its fellow of the right-hand side is reduced posteriorly so that it fails to reach the shoulder patch. Thus a white collar is formed. It is also interesting to see that at its anterior end a distinct constriction is present where the neck patch joins the ear patch of the right side. Fig. 3 shows a somewhat similar condition but the neck patch of the right side as well as

the ear patch is missing, while those of the left side are fully developed. In Fig. 4 both neck patches are missing, so that a white collar is formed. In dogs the neck patch is usually the first to drop out altogether, so that a white-collared dog is of very frequent occurrence. In fox hounds this patch is shown unusually well, either wholly or partly separated from neighboring patches. The separation of the ear patches, wholly or partially, so as to produce a white blaze or line in the middle of the forehead is about as frequent. In Figs. 8 and 12 a single neck spot only (as it happens, in one on the right, in the other on the left side) is still present but so slightly developed as to be only a small island of pigment wholly separate from the neighboring patches.

The crown spot is so often present in dogs as a little oval island, always on the top of the head about in line with the anterior bases of the ears (Fig. 4) that I am convinced it is a primary patch. It is common in bull dogs and bull terriers, and in other breeds is often seen but is so commonly not indicated at all, that it seems probable it is becoming lost, and its area is filled by the ear patches, since these are often separated by a very narrow median line only, which, as in Fig. 13, may continue posteriorly to separate the two neck patches medially as well. In other cases (Figs. 1, 6) the failure of the white nose stripe to extend farther posteriorly may be due to the persistence of this patch.

The demarcation of the side from the rump patches is indicated by the imperfect primary break across the lower part of the back in Fig. 4, while in Fig. 5, a similar primary break farther forward indicates the limits of the shoulder and side patches. In each case the break is incomplete transversely, with a narrow isthmus near the median line. In dogs there is a marked tendency for the ultimate centers of the side and rump patches to be close to the median line, so that the corresponding patches of opposite sides are confluent dorsally. This is especially the case with the rump patches, with the result that it is

very rare to see the two rump centers separated, but instead, as in Figs. 10 and 14, they appear, when much reduced, as a small median spot at the root of the tail. That they were originally paired, there is no doubt, as there is frequently (as in Fig. 9) a deep median notch indicating the median primary break between the centers, or (as in Figs. 11, 12) one of the lateral centers drops out, leaving its fellow of the opposite side. The continued union of the side patches with the shoulder patches is seen in Fig. 7, while in Fig. 9, though the union is still present between these patches of the right side, on the left side the shoulder patch has failed to develop, and the side patch is so reduced that it does not meet its fellow of the right. In Fig. 8 both shoulder patches are present more or less bilaterally equal, and, as frequently, are produced into narrow tongues on to the upper arm. The two side patches in Fig. 8 are also reduced, so as to be wholly separated from each other and from the neighboring centers. They are further interesting in being placed nearly median one behind the other instead of nearly opposite. In Fig. 11, on the other hand, they are far sundered, but this, in dogs, is a much less usual condition. In Fig. 10 a single median dorsal patch represents the slightly developed side patches, but whether this single patch corresponds to one or other of the two centers, or whether the two are actually fused in the dorsal line, I can not yet say.

The shoulder centers, when slightly reduced, are large in dogs, and cover a considerable saddle-shaped area, as indicated in Fig. 5, from near the center of the back forward including the fore leg and part of the fore shoulder. When further reduction takes place the pigment is drawn away from the extremities and the saddle separates from the neck patch (Figs. 2, 6) and then from the side patch (Figs. 5, 9), and finally the shoulder patches separate from each other (Fig. 8). One or other of the shoulder patches may drop out entirely (Fig. 10) or be reduced to a very small spot (Fig. 12) at what may be considered

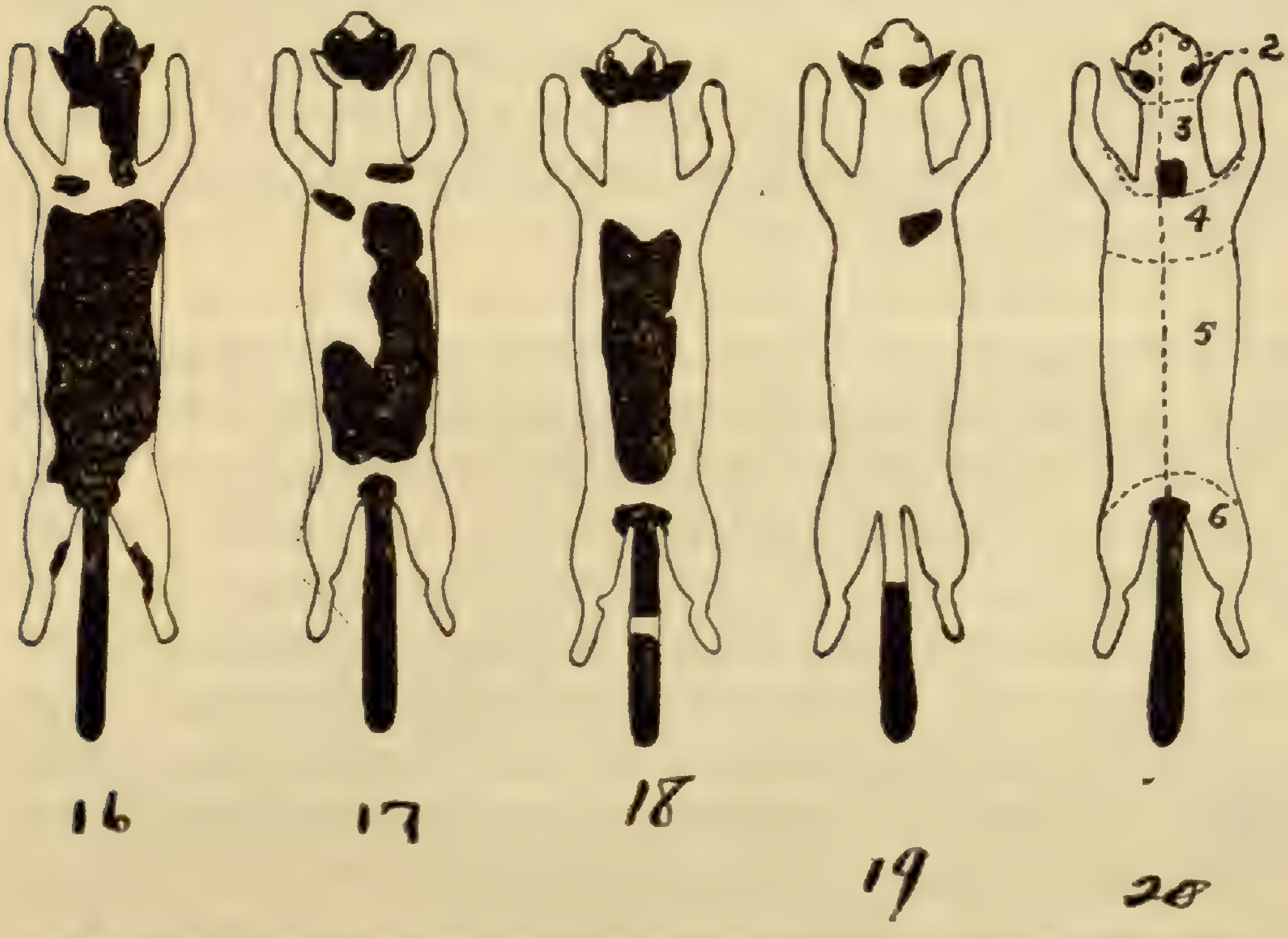
the ultimate center of the pigment patch, near the upper part of the body, near or just back of the shoulder. The ear patches seem to be the last to disappear, and these, too, may be variously reduced or only one may be present (Fig. 15). The approximate outlines of the patches when fully developed are indicated by dotted lines in Fig. 15, in which 1 is the crown patch, 2 the ear patch, 3 the neck patch, 4 the shoulder patch, 5 the side patch, and 6 the rump patch.

In dogs, there is seldom seen any tendency for these primary patches to divide. What has the appearance of such a tendency is seen, for example, in the coach dog, which is rather evenly flecked with rounded black spots, with often in addition, black ears and more rarely reduced rump patches. Fig. 9 shows such a dog in which both ear patches, one shoulder, both side and both rump patches are sharply indicated, though reduced. In addition there are present on the white body areas between, many small flecks of dark color, evenly distributed, which are clearly not islands separated from the primary patches. Indeed this spotting seems to constitute a wholly different category of pigment formation, in addition to that of the primary patches, which latter I have called "centripetal" pigmentation. As Professor Castle suggests to me, it is probably homologous with the "English" marking or spotted condition of domesticated rabbits, and possibly the dappling of horses is a similar phenomenon. When these spots and the primary color patches are of the same hue, it is not possible to distinguish the two in visual appearance, unless the latter are reduced areally, when, as is sometimes the case in the coach dog, one or more of the primary patches is seen with the spots, as it were, proliferating from its edge. This second element no doubt enters as a factor in the color pattern when the small spots are of a different color from that of the general body surface, as in case of the cheetah (*Cynælurus*) or the leopard and jaguar.

I am inclined to think that the excessive breaking up of

the primary patches, to be considered under the cow, is not a wholly similar phenomenon.

Five diagrams illustrating the domestic cat are shown in Figs. 16 to 20, and are interesting to contrast with



Figs. 16–20. Diagrams Illustrating Pigmentation in the Domestic Cat.

those of the dog, also a carnivorous mammal. The demarcation of the primary patches is usually less sharp than in dogs, but is in general similar. The most common appearance is where the primary breaks occur in the mid-line below, giving a white throat, chest or belly; or the separation of the aural centers produces a white streak on the nose or extends it up between the ears. The ear patches in Figs. 17, 19, 20, show successive reduction, so that at first the hinder margin of the ears, as in dogs, becomes white, then with further decrease in pigment production, the inner bases only are colored. The neck patch has its ultimate center farther back than in dogs so that when much reduced, it is present as a pigmented spot at the very base of the neck or even at the front of the shoulder (Figs. 16, 17). In Fig. 16 the neck patch of the right-hand side is only slightly reduced and is in contact anteriorly with the ear patch, while poste-

riorly it does not meet the shoulder patch. The left-hand neck patch, however, is quite separate from the neighboring patches and is reduced to a small area at the junction of the neck with the shoulder. It is absent in Fig. 17 from the left side and is represented on the right side by a similar small center, placed far back. In Fig. 20 the neck patch or patches show a reduction to a single small square median patch at the base of the neck, but whether this represents a median fusion of the two lateral centers, or whether one only has persisted and has shifted to the midline, I do not attempt to say, though the former hypothesis seems on the whole more probable.

The shoulder patch in house cats is relatively small, and, as indicated by the indentations in Figs. 17, 18, is of the fore side of the upper arm, but the shoulder patch when fully developed seems to cover the rest of the leg and a small scapular area. It is shown much reduced in Fig. 19, on the right-hand side, and is altogether wanting in Fig 20. The conjoined shoulder and side patches in Fig. 18 are shown reduced laterally, so as to form a broad median stripe which I take to mean that the ultimate centers are closely approximated dorsally. The neck patch is wholly absent, but both ear patches are present and joined medially. The sacral patches, as commonly, seem fused or at least very close together. There is a small break midway on the tail, which separates off a pigmented tip, a phenomenon which I shall refer to under "centrifugal pigmentation." The side patch is long comparatively, and extends forward to cover the deficiencies of the shoulder patch, as in Fig. 17. Here the left side patch has been reduced at its anterior end, and its separateness from the patch of the right side is indicated by the median indentations. It is often wanting in domesticated cats.

The sacral patches, pigmenting the buttocks and tail, seem to be fused or closely approximated at the root of the tail, as in dogs. I have seen no instance of the crown patch being shown in the cat, though such may occur.

The approximate boundaries of the five bilateral patches are indicated in Fig. 20 by dotted lines; 2 is the ear patch, 3 the neck patch, 4 the shoulder patch, 5 the side patch, and 6 the rump patch.

Among domesticated rodents the pigment patches have been studied in rats, house mice, and guinea-pigs. In all, the same patches appear except that in rats and mice the median crown patch appears to be lost, though in the guinea-pig it is often present. Diagrams of parti-colored mice are shown in Figs. 21–24, and sufficiently indicate

21 22 23 24

FIGS. 21–24. DIAGRAMS ILLUSTRATING PIGMENTATION IN DOMESTIC VARIETIES OF THE HOUSE MOUSE.

the primary pigment areas. The white spot on the forehead of Fig. 21 indicates a primary break between the two ear patches, and varies widely in different individuals, from a few white hairs only to a large blaze The inheritance of such a blaze has been studied by Little (1914). The white mark at the base of the neck in Fig. 21 indicates the beginning of separation of the neck from the shoulder patches and perhaps of the two neck patches from each other, because of its longitudinal extension. The white band across the neck in Fig. 23, however, indicates probably only the beginning of a separation of the neck from the shoulder patches, which in Fig. 24 has

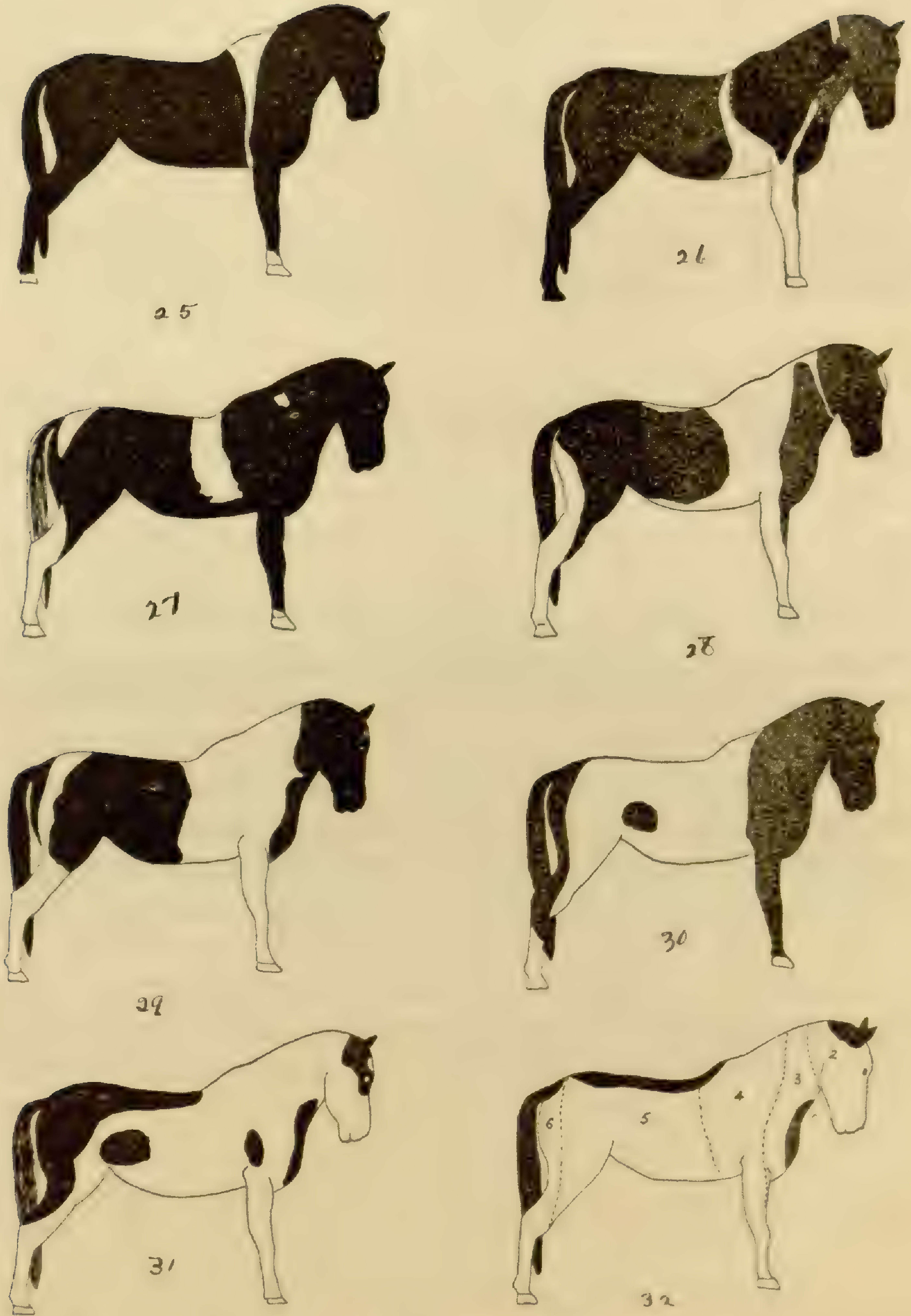
wholly sundered these two areas, so that a white-collared mouse results. The condition shown in Fig. 22 is similar, except that the separation has taken place on the right side only, between the neck and the shoulder patches of but one half of the body. A break between the two neck patches of opposite sides is further indicated in this figure by the deep median reentrant back of the ears.

In all four diagrams the areal restriction of the shoulder patches is shown, but in varying degrees. In Fig. 21, the pigment has not spread to the feet, leaving these white, and so in the other figures, but to a greater degree. A median linear break between the shoulders indicates the restriction of the patches of opposite sides at this point, which in Fig. 22 is more clearly perceptible. The posterior limits of the shoulder patch are further shown in this diagram, by the beginnings of a break between the shoulder and the side patches. In Fig. 24 this break is no longer interrupted, but clearly separates the two areas. Further, the side patch has dropped out on the left. In Fig. 23 an imperfect separation of patches on the posterior part of the body has taken place. On the right-hand side the shoulder patch, which in mice is of considerable extent, has broadly separated from the side patch, while on the left-hand side a long transverse break has taken place between the side and the rump patches, with two island-like white spots between, the anterior of which probably marks the transverse line of stress between shoulder and side patches, the posterior the median line of breaking between the two side patches. A slight indentation in the pigmented area far back on the right side of Fig. 22 points to the beginning of restriction between side patch and rump patch. The separation of these patches by a transverse mid-dorsal break is shown in Fig. 21, and their complete separation on the left side appears in Fig. 23 (the transverse white mark), while in Fig. 24, owing to the failure of the left-hand pleural patch to develop, the two rump patches, both partially separate from each other, are wholly disconnected

from the former except by a narrow isthmus on the right side. The long tail is usually without pigment, or mainly so where areal restriction is present, and it is seldom that pigment extends far on to the base of this member when the restrictive tendency appears. In the domesticated varieties of rats, the same patches may be distinguished. There is, however, an interesting variety known as the "hooded" rat, in which the ear and neck patches appear to be normal, but a narrow median dorsal area is pigmented for a varying length, sometimes quite to the root of the tail. A separate factor seems here to be involved, producing what may be called a "centrifugal" type of pigmentation, which in many forms of mammals causes a black spine stripe (*Sorex wardi, Tupaia tana,* certain forms of Apodemus, *Equus caballus*), and others.

Among guinea-pigs the typical primary patches are beautifully shown and may be seen in sundry figures published in papers by Professor Castle on heredity in this animal. The guinea-pig is one of the few mammals yet known in which the median crown patch is visibly present, a character which I take to be primitive.

In guinea-pigs the breaking up of the ticked color pattern has progressed under long domestication to an extraordinary degree, so that not only are black, tawny or grizzled animals produced in various shades, but even in the same individual, *the different primary pigment areas may be of different colors.* This fact is of much significance, for it indicates not only the mutual independence of the contiguous color areas, but further points to the manner in which a variegated color pattern may have been acquired. Among mammals the color pattern is in general, not greatly developed in comparison with birds, yet in many cases where some modification has taken place, it is evident that this differentiation is confined to the limits of one or two of the primary pigment patches. Thus in the South American Tayra (*T. barbara*), the head and neck are a grizzled gray, and the breaks occurring in pied individuals show that the grizzled condition



FIGS. 25–32. DIAGRAMS ILLUSTRATING PIGMENTATION IN HORSES.

is confined to the aural and nuchal patches only, for elsewhere the animal is black. In this case, too, the black condition is probably derived, for youngish animals are uniformly grizzled, and sometimes, apparently, this is the adult condition as well.

Among domesticated ungulates the same primary patches are to be distinguished in cases where partial albinism renders their bounds apparent, with the exception that in horses, cows and deer I have seen no clear indication of the median crown patch which in mammals is probably obsolescent.

In both horses and cows the patches show interesting and peculiar modifications. A series of diagrams (Figs. 25 to 32) show these patches in "calico" horses, though not so fully as could be wished. The first indications of areal restriction of pigment in horses appear in the shape of a white "star" or round spot in the center of the forehead. This is often accompanied by white at the base of the hoofs, or sometimes the entire foot is white producing the so-called "white stockings." But there is no necessary correlation between these white areas, such as Brewer (1882) tried to show. The white on the forehead may vary from a few white hairs to a broad blaze covering the entire front of the head between the eyes to the muzzle. Sometimes the restriction of pigment is such as to produce in addition to the white star on the forehead, a white spot over each eye, and sometimes these three spots are joined by a narrow unpigmented area. This indicates that pigment production is weak at a spot directly over the eye in comparison with neighboring parts, and this no doubt accounts for the fact that in black-and-tan or other dogs these are the pale spots over the eyes where black pigment is not produced. A white spot over the eye is also characteristic of many rodents.

Next after the restriction of the ear patches and the drawing away of pigment from the feet, the most common

white marking seems to be a primary break, as in Fig. 25, from the shoulder back of the foreleg, which delimits the posterior border of the shoulder patch. In the horse the shoulder patch is large, and differs from that of any mammal I have yet studied, in its great extent forward along the dorsal side of the neck nearly to the head. In Fig. 26 a small break at the back of the neck indicates the beginning of separation between the ear and the neck patches dorsally, and a long tongue of white running upward from the forearm indicates the anterior limit of the shoulder patch. This limit is marked still nearer the dorsal line in Fig. 27 by a white spot on the side of the neck near its base. In Fig. 28 the shoulder patch has entirely dropped out and the white space outlines very nearly its extent. The ultimate center is perhaps shown by the small shoulder spot in Fig. 31.

The area covered by the ear patches extends well on to the upper part of the neck, and in Fig. 29 is shown at its greatest spread, or, as in Fig. 28, cut off by a narrow white collar from the neck patch. The neck patch is remarkable from the fact that in its areal reduction it becomes restricted first dorsally, and the ultimate center of each side is nearly ventral on the throat, so that, as generally seen, the two centers form a single median patch on the front or ventral part of the throat. In Fig. 26 the neck patch is seen to pigment the anterior side of the forearm and is partly separated from the shoulder patch by a long tongue of white. It seems to extend up diagonally to reach the mid-line of the neck for a short distance only, as indicated in Fig. 28, where its bounds are only slightly contracted. In Fig. 29 it is so far lessened as to be absent from the forearm, though still in contact at the throat with the ear patch where, however, a deep indentation locates the dividing line between the two patches. In Fig. 31 a median ventral division of the conjoined neck patches is seen indicated at the upper part of the area, which in this case no longer reaches the ear patches. Still further reduction of both ear patches and neck

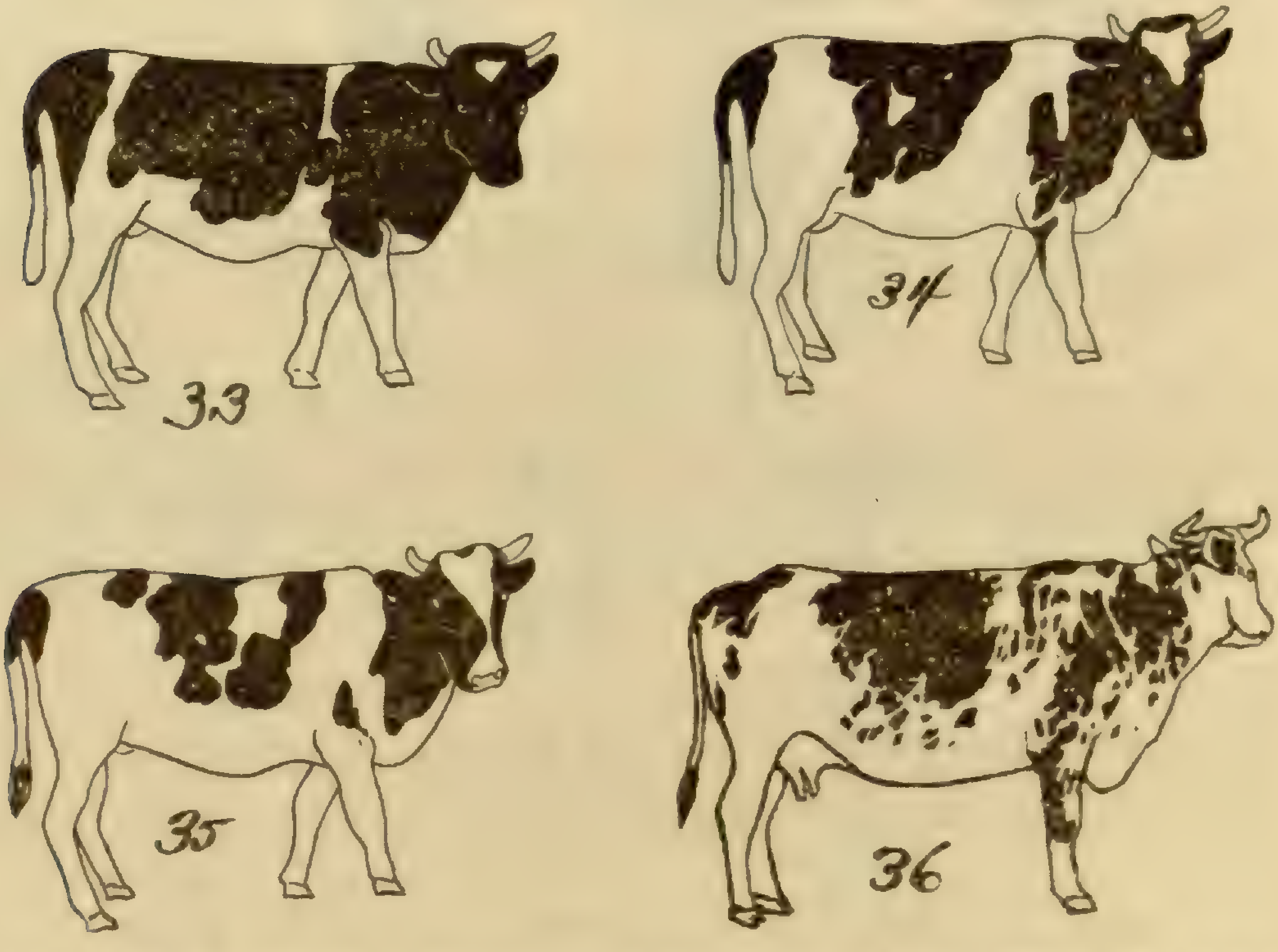
patches is seen in Fig. 32, but, as commonly, the neck patches seem fused in the midventral line. This shifting of the neck centers ventrally is a rather remarkable phenomenon which may have some relation to the manner in which the head is held erect. For this reason it might be expected also in antelopes, and is perhaps evidenced in such a species as the oryx, in which there is a black median line on the throat as though strongest pigment production centered there rather than on the gray sides of the neck. The median reduction of the shoulder patches in horses is sometimes indicated by a white mane.

The rump patches in the horse appear to be much as in other mammals, restricted to the tail and posterior part of the buttocks and the entire foot. In Fig. 30 the patch is shown at nearly its full development, except that it has failed to extend to the entire hind foot. In Fig. 27 it has drawn away still farther but remains in contact with the side patch at one place. In Fig. 29 it is further restricted to the tail and posterior border of the haunches, while in Fig. 32 it covers only the root of the tail and that member.

The side patch is the largest of all and extends from the shoulder to the fore part of the haunches and on to the fore part of the hind leg nearly to the foot, as seen in Figs. 27 and 28, where it is still in contact with the rump patch, or in Fig. 29 where it has become separated. In its further reduction this patch may appear as a small spot back of the ribs or, as often, a curious division takes place, separating the patch into a dorsal area and a lateral one. Occasionally this secondary break appears in a horse which has most of its patches otherwise well developed. In Fig. 31, the pigmented area of the tail, buttocks and lumbar region consists of the conjoined rump patch and a dorsal portion of the side patch, while the *ventral* part of the side patch is present as the oval spot at the groin. In Fig. 30 the latter spot only persists, but in Fig. 32 the dorsal portion of the side patch alone is present as a stripe along the entire back, except where it breaks away posteriorly from the small rump patch.

This peculiarity of the side patch in horses is somewhat paralleled in cows by a tendency to secondary breaking up, though in a different way, as detailed below. It is significant in this connection that in horses and donkeys there is usually a black stripe along the spine from shoulder to tail which may indicate that "centrifugal pigmentation" is also present (see beyond). The dotted lines in Fig. 32 indicate the approximate boundaries of the several primary patches. The crown patch seems to be wanting in horses; 2 is the ear patch, 3 the neck patch, 4, 5 and 6 the shoulder, side, and rump patches, respectively.

Of domestic ruminants I have studied the pigmentation in the cow and show in Figs. 33 to 42 a few of the many

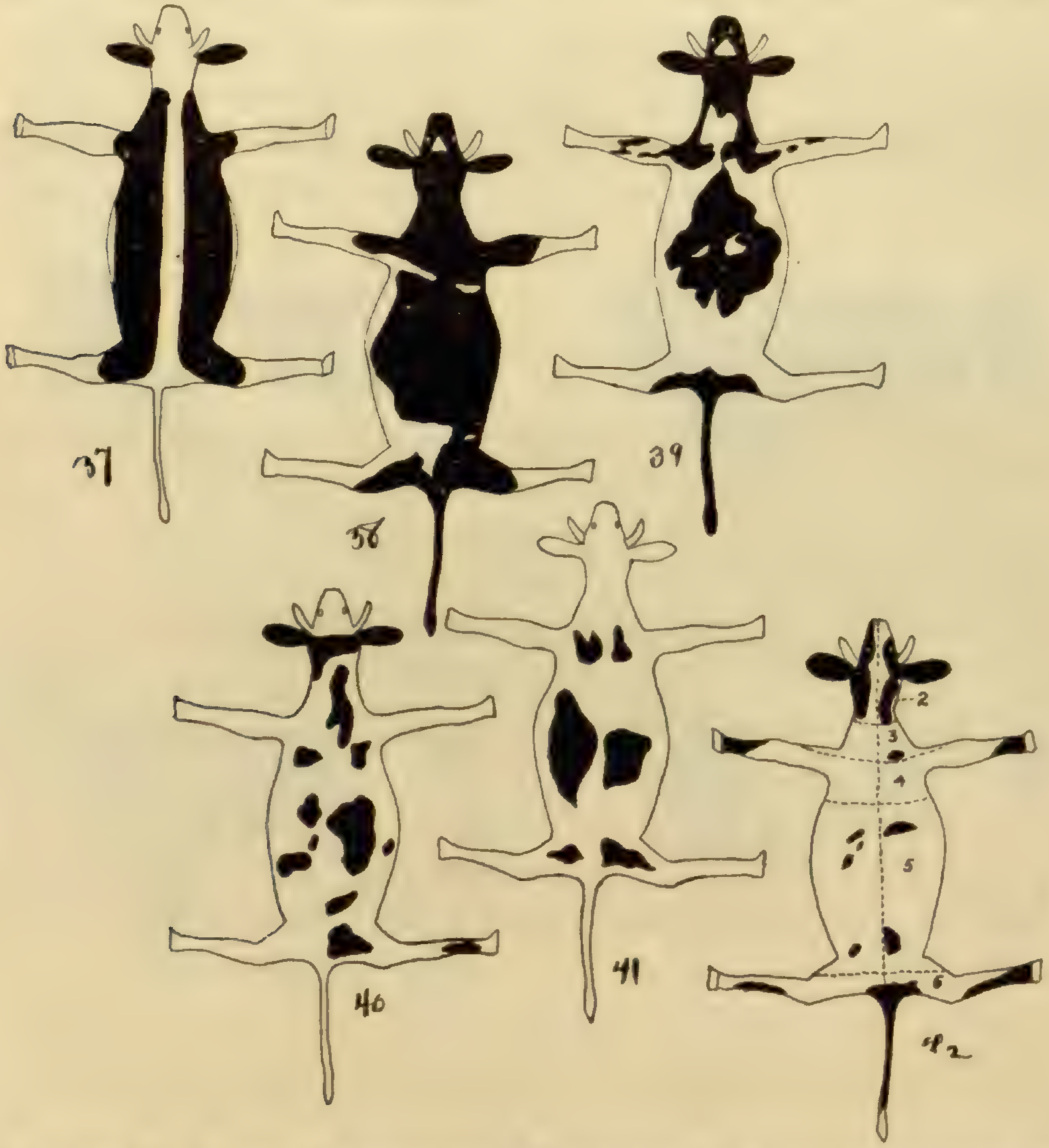


Figs. 33-36. Diagrams Illustrating Pigmentation in Domestic Cows, Side View.

variations in partial pigmentation. These are all drawn from photographs or from the animals themselves, and are of cows in which, so far as I know, there has been no attempt at breeding for pattern. Two types of spotting may be distinguished in cows: first, that in which the pigmented areas are sharply outlined and solid or at least

practically so; second, that in which there is a greater or less tendency for the primary patches to be much broken up into small islands (as in Fig. 36) by secondary breaks, though the main areas are still distinguishable. I take this second or fragmental type to be a different phenomenon from the diffuse or dappled condition seen in the coach dog or the dappled-gray horse.

In the cow, the ear patches as usual pigment each its proper side of the head to a short distance behind the



FIGS. 37–42. DIAGRAMS ILLUSTRATING PIGMENTATION IN DOMESTIC COWS, AS SEEN SPREAD OUT AND FROM ABOVE.

ears. The point of separation between ear patches and neck patches is indicated by a small break back of the skull in Fig. 38, while the posterior extent is shown by the two ear patches in Fig. 42. These patches usually

draw apart first across the forehead making here a triangular white mark, and on the muzzle, as in Fig. 34. Further restriction broadens these white marks and joins them by a narrow isthmus as in Fig. 35. In Fig. 40, the two patches are still conjoined across the vertex, but are much reduced, that of the right side more than that of the left. In Fig. 42 they have failed to join medially, though fairly well developed longitudinally. Still greater reduction, as in Fig. 37, confines them to the ears, the bases of which appear to be the ultimate centers.

The neck patch in the cow is more extended posteriorly than in the horse, and its center is strictly lateral rather than nearly ventral. It is shown in Fig. 34 somewhat contracted from the mid-line of the throat, but extends squarely back against the foreshoulder at the base of the neck, and is fused near its ventral corner with the small shoulder patch, itself much reduced. As in other mammals it appears to extend in its complete development, to the front edge of the upper foreleg. The animal in Fig. 41 shows a bilaterality in its pigmentation that is rather unusual. What appear to be the reduced neck patches are seen far back at the border of the foreshoulder. In Fig. 40 the left-hand neck patch has dropped out, but that of the right side is still present, though small, and in Fig. 42 it is reduced to a small spot only.

The shoulder patch in cows is remarkably narrow, and compressed between the neck patch and the body patch, whence it extends as usual on to the foreleg. In Fig. 33 a primary break back of the foreshoulder marks the nearly vertical posterior outline of the shoulder patch. In Fig. 34 the separation of this area from the neck patch is all but complete and the patch itself somewhat reduced. Its narrow vertical outline is thus indicated, as well as in Fig. 39, in which there is a narrow tongue-like extension down on to the center of the foreleg.

In its further reduction it appears as a small center at the base of the scapula, as in Fig. 35, or in Fig. 40, in

which both shoulder patches are present, though small. In Figs. 41 and 42 the shoulder areas are wanting. A very common mark in cows is a white belt just back of the foreleg. This is due to the development of a primary break between shoulder patches and side patches, a condition which is nearly realized in Figs. 33 and 38. It is probable that this marking has been more or less fixed through selection in breeding, and this has been the more readily accomplished, since this break occurs in a place which is one of the first in cows to cease pigment production.

The side patch is large and covers the entire lateral region of the body from the scapula to the hips, and on to the front edge of the hind limb. When only slightly reduced, it appears as a blanket-shaped area across the back as in Fig. 38, where it has not wholly broken away from the shoulder and rump patches, or as in Fig. 33, where it has become nearly separated. In its further reduction this dorsal blanket shows a peculiar manner of breaking up into more or less transverse stripes directed slightly backward. The beginnings of these secondary breaks appear in Fig. 39 in which are seen on each side posteriorly two deep indentations at the edge of the patch, whose points if extended would meet the white pigmentless islands already present within the patch. In Fig. 34 a similar series of indentations points to the trisection of the side patch which is realized in Fig. 35. Here is a characteristic which if developed might eventually result in the actual production of white stripes on the body, such as are found, for example, in certain antelopes as the bongo and the kudu. The tendency of the side patch to divide into three, as in these diagrams, is rather marked in cows, and even with further reduction the three centers persist fairly well. The first of these secondary centers is just back of the shoulder patch, the second about over the last ribs, and the third over the lumbar region. In Fig. 40 the first two are present on the left side, with a small spot between, which has become

separated from one or the other of them, while the third or lumbar spot has dropped out. On the right side, the first and second divisions are still fused dorsally, but the lumbar division is distinct. The same three divisions are seen in Fig. 35, better developed, whereas in Fig. 42, the two lumbars are present, one on each side, and considerably in advance of them, what seem to be the remnants of the first division of the side area, the left one of which has further broken up.

The rump patches show no especial peculiarities, but cover the posterior part of the buttocks and hind legs, and the entire feet and tail. Though frequently the two patches of opposite sides are conjoined medially, they are often, under considerable reduction, well separated. The beginning of such a separation appears in Fig. 38, where there is a deep median tongue of white anteriorly, marking the line of union. In Fig. 41 the reduction has progressed still farther so that the two patches are quite sundered medially and do not extend to the tail. In Fig. 40 the patch of the left side has become inactive, and that of the right side is small.

A curious condition not infrequently seen is shown in Fig. 37, in which all the patches are present, but those of the right side are separated from those of the left by a median dorsal white line, showing the distinct bilaterality of these pigment areas. In the figure, the ear patches are so restricted as not to reach the neck patches of their respective sides, the shoulder patches do not extend far on the forelegs, the side patches are reduced ventrally, and the rump patches, though in contact with the side patches, do not pigment the tail or extremities of the legs. A further reduction of pigment areas results in Fig. 41, in which the paired centers of neck, side and rump patches still appear.

The diffuse condition of pigmentation is illustrated in Fig. 36, which is a photograph, inked in. The ear patch is seen much reduced, but pigmenting the ear. The neck patch is of most irregular shape, with several subsidiary

spots separated from its lower border. A clear line separates the neck patch from the shoulder patch, which is also of most irregular boundary. The side patch, at its fore part, is broken into a series of small islands which tend to arrange themselves in lines following the direction of the ribs. The main part of the patch shows a decided tendency to break into the usual three or perhaps four portions. It is common for cows to have patches with very irregular boundaries and tongues of pigment, which may break off into isolated spots in a most bewildering fashion, but even in such cases it is possible to distinguish the main patches of which these form part.

White patches occur in other domesticated ungulates as the pig, the llama, the alpaca, the camel, the yak, the reindeer, and the goat. In the water-buffalo, occasional animals seen in Egypt show a beginning of pigment reduction through the presence of white in the forehead or on the tail. I have had no opportunity to study the markings of these species.

(*To be concluded*)

INTERNAL RELATIONS OF TERRESTRIAL ASSOCIATIONS

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I. INTRODUCTION

THE material here presented is based on the writer's studies, during the past five years, of terrestrial associations of plants and animals, mainly in different parts of the prairie region. The particular area chiefly used for illustration in this paper is the sand prairie of the Illinois River valley, plants and animals of which have been studied by Hart and Gleason (1907) and by the writer (1913*b*). A later study has been made of the vegetation of inland sand areas of Illinois (Gleason, 1910); the Lake Michigan beach area in northeastern Illinois has been studied by Gates (1912); beach areas in Illinois and Indiana by the writer (1914*a*). The chief representation of

the sand prairie is the bunch-grass association, well-developed in parts of northwestern, central and northeastern Illinois, and in northwestern Indiana, in each of which areas, as well as in the sandhills of Nebraska and of eastern Colorado, the writer has studied. Discussions of physical, vegetational and animal aspects of the associations of the central Illinois sand prairie, together with an annotated list of the animal species, with data on food, habitat-relations, life-history, etc., are embodied in the writer's paper (1913*b*), to which constant reference is made. Frequent citations to a more detailed study of local distribution of grasshoppers, in a Michigan area (Vestal, 1913*a*), and to the many associational studies of Shelford, are to be found.

The data which have accumulated relate nearly equally to the botanical and zoological aspects of associational study, but since the subject of plant ecology is at present more advanced than that of animal ecology, it has been possible to treat the vegetational side of the problem very briefly, so that more of the discussion relates to animals and animal assemblages.

The writings most frequently cited are indicated by italic capitals, the full titles appearing in the list of special references at the end of the paper.

The writer wishes to thank Dr. Charles C. Adams, Dr. Max M. Ellis and Dr. H. A. Gleason for suggestions and criticism.

II. INTERNAL ACTIVITIES OF THE ASSOCIATION, AS DETERMINED BY THE CONSTITUTION OF THE INDIVIDUAL ORGANISM

The internal activities of the association may be said to be the sum-total of the activities of all the plants and all the animals which make up the association. Such a sum-total of activities may well be thought of as an intricate and complicated mass of dependencies. It will simplify the treatment of the entire system of relations if the chief dependencies of the individual organism are first discussed. A knowledge of the ecology of the asso-

ciation is built up largely from a knowledge of the ecology of all the organisms which compose it.

A. Ecological Constitution of the Organism

The constitution of the organism is the sum-total of those of its characters which enter into relation with environment. These are commonly classified as *structural* and *physiological*. For the purposes of this discussion it would seem preferable to subdivide physiological characters, restricting the term *physiological* to denote those characters concerned with ordinary metabolic processes of the organism, and excluding those having to do with life-history and rates of reproduction (these may be distinguished as *biographical* and *numerical*[1]) and also, when dealing with animals, those related to behavior (*psychological* characters). The constitution of the organism in relation to environment will be discussed in terms of these classes of characters.

B. Constitution of the Plant in Relation to Environment

The environmental influences in the association are of three kinds: (1) physical, (2) plant, (3) animal. Each plant and each animal must obtain from each of these three constituents of its environment certain necessaries; it has certain structural and physiological characters which enable it to obtain these necessaries, and to withstand adverse environmental influences.

The environmental relations of plants are very different from those of animals. A tabular comparison of these relations has been made by Shelford (*A:* 593). As therein pointed out, structural characters are of greatest importance in the adjustment of the plant to the environment, and plants in a given habitat are likely to have a common structure or growth-form, indicating common or ecologically equivalent physiological conditions within.

Different plants (and different animals), within a com-

[1] Based partly on Forbes', classification of adaptation to food requirements (1909: 292).

mon habitat, are similar in ecological constitution (ecologically equivalent) in so far as their presence is determined by the same environmental conditions. It should be pointed out that there are local environmental differences within the area of the association which allow the presence of differently constituted organisms, and that the entire range of environmental conditions within the habitat is usually much wider than that of the environmental complex selected by a particular organism. The environmental complex of the organism is not the same as the sum-total of environmental conditions within the association. Each organism differs in greater or less degree from others in ecological constitution, and thus selects a different environmental complex.

The physical factors of the environment are of greatest importance in the life of the plant. Plants influence one another directly to only a slight extent. There is usually very little of the social relationship among ecologically similar plants which will compare with such relationships as seen in animals. Competition among plants is mainly a struggle to determine which plants are to be most favored by physical conditions, and it is probably most severe for the physical factor present in minimal quantity. In desert associations plant competition is almost exclusively for water, and extensive root systems are developed. In grassland it is very largely for above-ground space; in forests it is principally for light. The influence of the animal-environment is probably of greater importance than has commonly been realized by plant ecologists; the study of economic entomology and of the effects of grazing upon grasslands is helping to bring about a realization of the importance of animal influence upon plant life.

The structures of plants show frequent and great modification in response to the physical conditions of the environment. These modifications are most frequent and important with respect to the factor present in minimal quantity. Characters which may be associated with

direct plant influence are infrequent. Certain plants which become more abundant as a result of close grazing are equipped with spines, or have acrid or pungent juices; and many other characters may be correlated with animal influence. The structural modifications are most evident in the adjustment of the plant to external conditions, though these are accompanied by physiological characters which are also in harmony with the environment.

C. Constitution of the Animal in Relation to Environment

The animal, like the plant, selects an environmental complex which is of three kinds: (1) physical, (2) plant, (3) animal. Different animals show extreme variation as to the degree in which the different parts of the environment are important to their existence. Endoparasites, for example, are most directly concerned with the animal part of their environmental complex.

The existence of any animal is dependent upon a number of physical factors, all of which must be present in proper degree or quantity. Minimal and maximal quantities of any one of several factors mark the limits of existence of any animal (*A:* 598—law of toleration of physical factors). It is not necessary to consider these factors in detail. The animal reacts to physical environment most evidently by its behavior: psychological characters restrict activities more narrowly than do those of other types. They are accompanied by structural and physiological characters; hibernation, storage of food, etc., are biographical characters correlated with seasonal changes in physical environment. Animals which are subjected to very severe physical conditions may produce a larger number of offspring than those to which physical conditions are favorable. This is an example of correlation of a numerical character with the physical environment.

The plant environment reacts upon and modifies physical and animal environments, and has also direct influ-

ence upon the animal. In addition to its effect in the control of temperature, light and other physical factors, the vegetation constitutes the basic food-supply for the animal community, and also provides shelter and materials for abode (*A:* 601). Cases of direct association between particular plants and particular animals are numerous, but the majority of animals have no direct relation to particular kinds of plants. Behavior characters are in general of greater importance in the relation of the animal to the plant environment, though such relations are not confined to psychological characters.

There are two sets of relations between the animal and its animal environment. These are: (1) *social,* and (2) *antagonistic.* Social relations (*inter-psychology* and *inter-physiology* of Shelford, *A:* 608, *b*) include those between individuals of the same species, and between animals of the same or similar *mores*[2] (ecologically equivalent animals), in so far as these relations are not antagonistic. Breeding and family relations are the principal activities which come under this head. Behavior characters are of greatest importance, as compared with structural and other characters. The antagonistic relations constitute the *intermores-psychology* and *physiology* of Shelford (*A:* 608, *c*). They are the antagonistic relations between animals not ecologically equivalent, and they are also antagonistic relations within a species and between ecologically similar forms. These relations are probably not greatly concerned with reproduction, but center about the feeding activities of the animal. The existence of the individual animal, in its relation to other organisms, is dependent upon three conditions: (1) it must obtain suitable and sufficient food, (2) it must be free from destructive competition of animals of similar requirements, (3) it must be able to escape or to withstand attacks of other animals (or, sometimes, of parasitic fungi or bacteria). The various characters of the

[2] *Mores* (Latin for customs, habits) has been used by Shelford (1911*a*: 30) to supply the need for a term including all physiological and behavior characters of the animal.

animals are correlated with all three of these conditions. The characters are both "adaptive" (fixed by heredity), and regulatory (not fixed).

Following is a synopsis of correlations between the various types of characters and the three conditions of existence, in the relation of the animal to its antagonistic animal environment.

(I) *Characters Which Enable the Animal to Obtain Food*

1. *Structural Characters.*—Animals of selective food-habits often have specialized structures, as in the case of the long tongue of woodpeckers. Animals of non-selective food-habits have mouthparts that are not so highly specialized; thus grasshoppers and cutworms have heavy mandibles for cutting vegetation; tiger-beetles and *Chrysopa* larvæ have sharp piercing mandibles. The whole structure of the predaceous animal, its "action system," is sometimes suggestive of the manner of pursuit or holding of its prey.

2. *Physiological Characters.*—The physiology of animals of different food-habits differs materially. Physiological characters are not apparent, generally speaking, and are secondary to psychological characters. The range of food assimilable by the animal is usually much wider than that selected by it, as is seen when animals of selective habits take new kinds of food when the usual food is exhausted, often thriving seemingly as well as before.

3. *Psychological Characters.*—Selection of food is determined chiefly by behavior characters of the animal. These may be so widely variable that the animal will be virtually omnivorous, as in the case of crickets, or so narrowly restricted that it eats only a single species of plant or animal, as the leaf-beetle *Blepharida*, a sand-prairie insect eating leaves of the three-lobed sumac, and the pentatomid bug, *Perillus*, which feeds on *Blepharida* (cf. *E:* 49, 30). Selection is only one of the many psychological characters relating to food. The behavior characters manifested in obtaining food are of great variety.

With these are accompanying structural and physiological characters, which, however, play a subordinate part.

4. *Biographical Characters.*—These may consist in timing the life-history of the animal with that of the food-species (plant or animal) in such a way that the period of greatest activity of the former coincides with the period of greatest growth or abundance of the latter. This feature may be incidental to seasonal change of physical environment. Whatever its cause, it is very general in an established association, so general that it is seldom recognized. It is of advantage to both animal and food species.

5. *Numerical Characters.*—The rate of reproduction must be so adjusted to its food-supply (plant or animal) "that only the unessential surplus of this food shall be appropriated, leaving the essential maximum product undiminished" (Forbes, 1909: 293). Species of restricted food-habits must remain less numerous in individuals than general feeders, as the available food-supply is very much less.

(II) *Characters Which Remove the Animal from the Competition of Other Forms*

1. *Structural Characters.*—Structures which permit animals to live in varied habitats, to take varied foods, or to time their activities differently, remove each group of animals from competition of all the others, resulting in advantage to all. To that extent the fossorial forelegs of the mole, the long proboscis of the butterfly, and modifications of the eyes of nocturnal animals, are characters which do away with competition. The structural characters are, however, accompaniments of modifications of behavior, and are secondary to the latter.

2. *Physiological Characters.*—Ability to digest food-materials unavailable to other animals is an advantageous physiological character. Thus the leaf-beetle *Chrysochus auratus*, which lives on dogbane (*Apocynum*), and the "skin-beetle" *Trox*, which eats animal tissues in an advanced stage of decomposition, have few com-

petitors for food. Physiological, as well as structural, characters, are accompaniments to modifications of habit.

3. *Psychological Characters.*—Apparent preference for certain activities, certain habitats, or certain foods, together with peculiar behavior complexes, seem to be of greater importance in removing animals from competition than structural and physiological characters. Highly regulatory habits permit certain animals to adjust themselves to changing conditions of competition.

4. *Biographical Characters.*—Professor Forbes (1909: 295–298) discusses the alternative timing of the active period among close competitors for food. (It so happens that the animals mentioned, having almost identical habits, compete with each other in many ways, besides with respect to food.) In the sand prairie it has been found that different species of certain genera, having otherwise the same habits, differ greatly in life-history. Evidence of this biographical adjustment is more or less complete for two species of *Arphia* (*E:* 21), two or three species of *Hippiscus* (*E:* 21), two species of the milkweed beetle, *Tetraopes* (*E:* 47), and three species of *Proctacanthus*, robber-flies (*E:* 55). In these genera the term of activity of one species is abruptly followed by that of another, the successive periods usually covering most of the summer season.

5. *Numerical Characters.*—When a certain limited food, place of abode, or other desideratum is used by two or more kinds of animals at one time, a numerical adjustment is likely to be found among these competing species. The rate of multiplication of each species must be sufficient to keep up its numbers, to allow it to hold place with competing species. (Too high rates of multiplication, on the other hand, are disadvantageous because of other influences.)

(III) *Protective, Defensive and Concealing Characters*

1. *Structural Characters.*—Animals have various defensive, protective and concealing structures. Stings, beaks, mandibles, teeth, claws, hairs, spines, resemblance

to surroundings in color or form—all are of advantage to animals which possess them. Certain of the interstitial or blowsand animals resemble in color the sand on which they rest (*Cicindela lepida, Stachyocnemis, Psinidia, Spharagemon;* cf. *E*).

2. *Physiological Characters.*—Malodorous and ill-tasting animals are to a considerable degree exempt from attack. This is essentially a physiological modification, though a structural basis in the form of glands may be present. In the sand prairie *Chrysopa* (lace-winged fly), a number of *Hemiptera,* ladybird beetles, soldier bugs (*Chauliognathus*), blister-beetles (*Epicauta*), and others, are ill-tasting (perhaps not to some animals). The skunk's lack of caution is well known.

3. *Psychological Characters.* — Self-preservation in animals depends more upon their activities and behavior than upon special structures. The ordinary methods of resisting or evading attacks of enemies are generally known and need not be discussed. Many specialized instincts have arisen, such as feigning death, or dropping to the ground when disturbed, as seen in many herbicolous beetles.

4. *Biographical Characters.*—It is to the advantage of animal species preyed upon by others if their period of greatest abundance is timed with the period of greatest activity of the animals which feed upon them.

5. *Numerical Characters.*—Animals, as well as plants, must produce a normal excess in numbers which will provide food for other animals and still leave a sufficient number of individuals to continue the species.

It will be noted that the various kinds of characters usually accompany one another, all being parts of a single modification. This modification may have relation to one or to several of the environmental influences (physical, plant or animal) or to more than one kind of antagonistic relation between the animal and others. The modification is not necessarily advantageous to the animal with respect to all or to any features of the

environment, though a large number of characters do result in advantage. Characters advantageous in one relation may be disadvantageous or indifferent in another relation. The origin of the characters is not at present a subject which can be treated in a study of interrelations of organisms (cf. Shelford, 1912*b*: 342). Behavior characters appear to be of greatest importance to the animal in determining its relations with other organisms of the association, though usually these are accompanied by physiological or structural characters. The animal is not *adapted* to a particular status in the association; its ecological constitution determines what place it shall be able to find among the other animals of its surroundings. The relations among the various animals, when a state of equilibrium has been reached, are the result of mutual accommodation on the part of all the animals involved.

D. Internal Activities of the Association

It has been indicated that the complex of activities within the association is the synthesis of all the activities of the individual organisms. Each plant and each animal is subjected to physical, plant and animal influences. From the extreme complexity of the entire system of relations within the association, it is hardly possible to consider more than one or several of these at one time.[3] It is possible, however, to see that each species finds a status within the association, according to its particular combination of internal and external relations. It continues in fairly constant numbers from year to year. A change in these numbers, if at all great, may cause a disturbance in the association, which is quickly regulated by the activities of conflicting organisms (Forbes, 1880). The entire association of plants and animals, by very

[3] Very helpful diagrams are given by Shelford (*C*: 167, 168) which illustrate the food relations of land (prairie) animals. There are also diagrams showing food relations of aquatic animals (*C*: 70, 71). Food relations of animals of plains and mountain streams are discussed by Ellis (1914: 122–127; diagram on p. 125). References to studies dealing with interrelations of organisms may be found in the recent handbook of Adams (1913: 123 et seq.).

reason of the conflicting interests, the varying conditions necessary for existence, and the varying methods of response to these conditions, forms a self-contained and self-regulating system of activities.

III. RELATIVE INFLUENCE OF DIFFERENT ORGANISMS WITHIN THE ASSOCIATION—DOMINANCE

The plant ecologist determines which plants in an association are of greatest importance (dominant) by observing which species tend to increase at the expense of others, which are most abundant, most frequent, largest, etc. Competition among plants in a grassland association is mainly for space, and the dominant species are usually determined with considerable accuracy after some study. With the animals the consideration of dominance involves greater complexity. The important relations between conflicting animal species are those in which they obtain food, are removed from competition, or escape enemies. These relations are in each case most directly concerned with food. The plant-eaters of the association thus form a dominant group within the association, since predaceous and parasitic animals, and scavengers in large part, depend upon them for existence. Individual species within the various food-groups, however, present such striking differences in importance, that we can not speak of all plant-eaters as dominant forms, or that all animals of other food habits are unimportant. It is merely probable that the phytophagous group will contain a larger proportion of dominant species. This appears to be the condition in the bunch-grass association.

A. Factors of Dominance Among Animals

The success of an animal species within an association is due to the resultant effect of a large number of factors. Among these may be mentioned number of individuals, size, activity, voracity, concentration of food, rapidity of growth, rapidity of reproduction, and wideness of distribution in space and in time. Dominance signifies more

than mere ability of a species to thrive in its surroundings: the species of greatest influence are those on which the greatest number of other animals depend; thus dominant species are successful, but successful species are not always dominant. Species which are relatively free from competition or which have comparatively few enemies may be successful, but are not dominant, and are usually not numerous. Species which are successful and at the same time extremely abundant, usually form the food of a large number of other animals, as it appears to be the rule that no considerable source of food within the association is left unused. Dominance in a species, then, would seem to include the dependence of other animals upon it, plus the ability to thrive in spite of the drain upon its numbers.

B. Criteria of Dominance Among Animals

The factors mentioned as contributing to the success of a species, and the numbers of animals dependent upon the species, are all indications of the degree of its dominance. It appears that another criterion is available, which perhaps expresses the summation of many factors which contribute toward dominance. This is the degree of specialization exhibited by the species in its adjustment to a particular place in the association. Dominant animals appear to be those of moderately specialized habits rather than those of highly specialized, or relatively unspecialized, habits.

C. Specialized and Unspecialized Animals

Each species may be referred to a position in the scale of specialization in habit. The degree of specialization of the species is well seen in the food-habits, though all the habits are to be considered. The most abundant food in the sand prairie is plant material, bunch-grasses. The majority of the plant-feeders are adapted to eat herbage of nearly any kind: they are not restricted to particular species or particular parts of plants. They are non-selective feeders. Grasshoppers, cutworms and certain

leaf-beetles are thus moderately specialized plant-eaters. There are also non-selective predaceous animals, as tiger-beetles and lycosid spiders, which eat any kind of small animal. These are also moderately specialized. The moderately specialized animals carry on the gross metabolism of the association; they constitute the dominant group, and include the dominant species.

Selective feeders belong with the highly specialized animals. In the bunch-grass association *Languria bicolor*, an erotylid beetle, bores in the stems of the composite *Cacalia* (Indian plantain), while *Lygæus bicrucis* (hemipterous) feeds on the same plant; *Perillus circumcinctus* eats *Blepharida rhois*. Others of the association eat selectively. The majority of parasites are greatly restricted in their selection of hosts. Such animals are particularly dependent upon special kinds of food, which in many cases are not available to general feeders. Highly specialized forms are thus enabled to avail themselves of opportunities denied to animals of generalized type; but while they avoid competition by the adoption of special kinds of food, or by special habit of some other kind, they lack the versatility of the less specialized animals, being unable to adjust themselves to changed conditions. They may, therefore, become abundant at times; but as they depend wholly upon one variable condition (perhaps the presence of a particular plant species, which may be quite infrequent) they never can become dominant species. Absolute numbers of the insects which live upon *Cacalia,* for example, are insignificant in comparison with such animals as the grasshoppers.

On the other hand, animals of relatively non-specialized habits would also be ineffective in the association, for whatever field of activity they were to enter, they usually would find already occupied by some animal better constituted for that activity. Such non-specialized forms would assume particular importance only when some animal on which they might feed should become unusually

abundant. Few animals are really non-specialized in habits; many moderately specialized species, however, may on occasion turn from their ordinary activities, perhaps to appropriate a particularly abundant kind of food. Many ants are thus habituated to certain ordinary kinds of food, but are able to eat organic food of almost any sort, and do vary their food with circumstance. When, as frequently happens, some animal species becomes very abundant,[4] the attacks of a great many species of flexible habits becomes concentrated upon it, and the numbers of the food-species are soon reduced to normal. Animals with non-specialized habits, by taking whatever food is easiest of access, act as regulators of disturbances within the association. A clear exposition of the manner in which species of generalized habits restore unbalanced conditions to equilibrium is given in a paper by Forbes (1883), in which the regulative action of birds upon insect oscillations is discussed.

The animal's status within the association is determined not only by its food-habits, but by the sum-total of its physiological and behavior characters (its mores). The degree of dominance is indicated not merely by the degree of specialization of food-habits, but in all habits, by the degree of flexibility of behavior. An extreme specialization in nearly any behavior character, as habit of abode in the pit-digging ant-lion larva, prevents the species from becoming dominant. The degree of specialization of behavior is thus a convenient criterion of the relative influence of animals in the association. The dominant animals are moderately specialized, and carry on the ordinary work of the association. The highly specialized animals make use of space otherwise unoccupied and food material not demanded by other species. Certain of the first group, with habits more highly regulatory than is usual, with perhaps some few unspecialized forms

[4] With some animals sudden abundance is a matter of seasonal periodicity, as in the case of May-flies (Hexagenia) along the Illinois River (*E*:17). The adults on emerging become a sudden source of food for animals of adjoining terrestrial associations, as the bunch-grass.

in addition, tend, by following the path of least resistance, to act in opposition to forces tending to destroy the biotic equilibrium.

IV. Distribution within the Association

The association may be subdivided into minor groups of organisms, both in space and in time. Each group, being thus removed from the immediate influence of the others, is to some extent self-contained, having its own environmental conditions, its own assemblage of organisms, and its own system of interrelations.

A. Distribution in Space[5]

Different parts of the space occupied by an association present different environmental conditions. In the vertical distribution, four strata, the air (cf. *E:* 73), the plant layer, the surface layer and the underground layer, are usually present. In forest associations, the plant layer is complex, plants of various heights giving rise to minor strata (cf. *A*). In grassland associations the plant layer is relatively uniform. Animals are most numerous, during the feeding activity, in the plant layer. Others find food at the surface or underground. Many of the animals in the air or on the ground move about rapidly from plant to plant. Predaceous animals (while active) are frequently permanent members of air and ground layers, depending for food upon the transient animals and upon members of their own group. The ground stratum is composed of the surface and subsurface layers (*E:* 72), which are not, however, continuous horizontally, but alternate to greater or less extent.

Local variability in horizontal distribution is due partly to local discontinuity of the various strata. This interruptedness is particularly conspicuous in open associations, where the plants do not form a dense growth, but are separated by open spaces. The subsurface area is provided by cover of various kinds, which lies more or less scattered about on the surface.

[5] Cf. Shelford, *A, B,* 1912*b*, *C*; also *D*: 167; also p. — of this paper.

The motility of the animal allows change in stratum, and to some extent and in some animals, in habitat, with change in activity. The food-stratum and the food-habitat are apparently of greatest importance in the relation of the animal to other organisms.

B. Distribution in Time

Physiological activities of the plants are subject to diurnal variation, and are also greatly affected by variations in weather conditions. The greater part of the animals of an association are active during the day. Others are nocturnal. During the inactive period of the day the animal rests in some more or less sheltered place, perhaps in a burrow or nest. The inactive state is also induced by unfavorable weather conditions.

Seasonal changes in the association are very great in temperate climates, particularly in treeless regions, where the winters are severe. Seasonal changes in the vegetation are marked, certain groups of the plants appearing in successive periods during a summer season, giving four or five successive *aspects* to the plant cover. A corresponding seasonal distribution is observed among the animals of the association (cf. *D:* 175).

Annual changes in the associations are indicated by the very marked differences in the numbers of individuals, in certain species of plants and animals, in successive years. This may be due (1) to fluctuation in the numerical adjustment between different organisms, and (2) to the effect of annually varying phenological conditions upon the various organisms.

Oscillatory irregularities in the association take place at indefinite intervals. The causes and nature of oscillations have been thoroughly treated in several of Forbes's writings (1880, 1883, 1887).

V. INTERDEPENDENCE OF TERRESTRIAL PLANT AND ANIMAL COMMUNITIES

The thesis of the following section is that, in terrestrial climatic or extensive environments, the relations between

the assemblage of plants and the assemblage of animals are intimate and regular of occurrence; so much so that (1) the two are coextensive, (2) the two constitute together a community which may be called a biotic association, (3) neither plant nor animal assemblage usually occurs independently of the other, (4) the geographic distribution of many of the plant and animal species which make up the assemblages are in general correspondence, (5) the species composition of the association, over its range, varies no more widely, relatively speaking, than would an assemblage of plants alone. Perhaps the single view-point of the botanist, on one hand, and the zoologist, on the other, has tended to a neglect of the dual character of the one problem. Probably most botanists and zoologists agree that relations of animals and plants within a habitat are most intimate, and there is a tacit assumption that all the organisms in one place constitute the true system of interrelations, but botanists have spoken of plant communities, and zoologists of animal communities. There are numerous disharmonies and variations in agreement of plant and animal assemblages, but these must not be allowed to obscure general facts of correspondence.

It is recognized that plants and animals of an area of essentially homogeneous physical conditions are interdependent, the animals as a group being wholly dependent upon the plants for food, and many of the plants being directly dependent upon animals, as in the matter of pollination. All are directly or indirectly affected by animals in some way. It is also recognized that the plants are a good index to conditions for animal life, the plant assemblage affecting animals locally in modification of the physical environment, and more directly in providing food, shelter, etc. (*A:* 601). It is further accepted that plants and animals respond to general environmental conditions in similar manner (Craig, 1908). Thus considered, the character of the plant population of an area is an index to general character, or ecological

type, of the animal assemblage. These relations, however, are quite general, lacking detail. Detailed considerations may be *geographic,* including geographic range of species and of communities, and the distribution of species and of individuals into communities; and they may also be *local,* dealing with interrelations of plants and animals within the area of the community.

A. Geographic Relations of Terrestrial Plants and Animals

1. *Geographic Range: The Province.*—If one were to plot the geographic range of the plant species found together in a given climatic habitat, a general correspondence in distribution would be made apparent, a large number of the species ranging more or less continuously over a common, rather definite area (cf. Transeau, 1905). The similar ecological constitution of these plants and their consequent selective distribution into similar environmental complexes gives a uniformity to the vegetation over the geographic region in which these environmental conditions are found, and the resulting vegetation unit is known as a *vegetation province* (Gleason, 1910: 42). The area of the province is generally uniform in physical conditions. This uniformity is only relative, being subject to gradual geographic variation in climate, perhaps giving rise to subregions in distant parts of the province, and to abrupt local variations in soil, water-content, exposure, etc., giving rise to local or edaphic plant assemblages very different from those of the climatic or geographic type. Thus the prairie province occupies the winter-dry interior region of North America. Environmental variations from east to west, climatic and physiographic, divide the province into the three subregions of Pound and Clements (1898). Certain plant species range over one or all of these subregions, still others establishing themselves over the whole area of the province and also scatteringly eastward, in dry treeless parts of the deciduous forest province, to the Atlantic coast. These last are also typical prairie plants, though

extra-limital in parts of an adjoining province locally approximating the prairie environment.

The habitat-selection of different animal species results, in precisely the same manner, in similarity of geographic range among ecologically similar animals. These correspondences of distribution point to the existence of definite areas characterized by general similarity of the animal assemblages. As the physical factors of the environment are the same ultimately for animals as for plants, and as the vegetational environment for animals has the same range as the physical environment, we might expect animal communities to have the same geographic distribution as plant communities, and we might expect the area of the plant province to be characterized by distinctive kinds of animals as well as by distinctive kinds of plants. The province is thus not simply a vegetation province, but a *biotic province.* This is not a new notion. Ruthven (1908: 388–390) has stated a current viewpoint as follows:

> Those who are acquainted with the literature of the field zoology of North America are familiar with the fact that, since the time of the Pacific Railroad surveys, naturalists have noted that there are in North America well-defined biological regions. These have been pointed out at various times by Allen, Cope, Merriam, and others, and the fauna of each has been more or less investigated. . . . For example, we have forms of birds, reptiles and mammals characteristic of the southeastern deciduous forest region, and still others characteristic of the northeastern coniferous forest region, etc.

Shelford (*A:* 604) bases his classification of animal regions upon that of plant regions, as worked out by Schimper (1903) and Transeau (1903, 1905).

How close the correspondence of distribution of particular animals with that of vegetation provinces may be, is well shown in the case of North American rabbits (Nelson, 1909). The distribution maps shown for certain species and groups of these animals might almost serve as maps of the provinces. Many other animals, vertebrate and invertebrate, correspond in area with the plant provinces. Among the insects listed by Hart (1907: 205)

as western species, those for which a number of locality records are available are plainly to be assigned to the prairie province, the range of most of them extending west to the Rocky Mountains, north about as far as Montana, east to Illinois or Indiana, and south to Texas.

Other animal species bear apparently no relation to province boundaries. Such animals have been discussed by Shelford (*A:* 606, footnote), who shows them to be of three types: (1) Species of scattered but very wide range, covering perhaps several plant realms (animals of local associations of extreme habitats); (2) Species occupying only a part of the plant realm in which they belong (animals of such ecological constitution that their range is restricted by some conditions unfavorable in certain parts of the province); (3) Species occupying intermediate ground between two realms—these are few (Ruthven). These exceptional species are found also in plants, so that local associations are occupied by both plants and animals of the scattered-but-wide type of range, while certain subregions, as the Great Plains area of the prairie province, contain associations with both plant and animal species restricted to these less extensive areas.

Associations of two adjoining provinces may intergrade, if ecologically similar, or may alternate if dissimilar. Similar associations of two provinces may contain the same or closely related species, as with certain grasshoppers which range in both northeastern and western coniferous provinces (*D:* 173). But these same associations contain also plant species in common, so that irregularities of range are no greater in animals than in plants.

2. *Distribution Within the Province: Distribution of Plants and Animals into Communities.*—It is seen that plant and animal species may correspond closely in geographic range. There may be also more local correspondence in distribution. The plant community has been found by the writer to be the convenient index of the

area of the habitat for animals. It has been observed, in an area in Michigan, that grasshopper species correspond closely in local distribution with plant communities (*D*). There is evidence that local distribution of animals is seldom promiscuous as a result of motility (*D:* 159). It appears also that the local variability of environmental conditions within the area of the climatic plant community is sufficiently great, usually, to supply all necessary conditions for a large number of animals, so that the limits of the plant community need not be passed, ordinarily.

> The animal community of the area may be thus, in large measure, self-contained, and coextensive with the plant community (*D*: 161).

One of the problems of plant ecology has been the differentiation of plant communities or associations. Mere comparison of lists of species is not sufficient; relative abundance of various species must be considered as well. Animal assemblages in contiguous areas must be separated in the same way. Given two adjoining habitats differing in plant population, it has been found that, in addition to differences of animal species,[6] there are also differences of relative abundance in those animal species common to the two areas (*D:* 154, 167).

The local area of a plant community is determined by (1) local distribution of the physical environmental complex, and (2) influence (competition, etc.) of adjoining plant communities. Local area of the animal community depends upon (1) local distribution of physical environment, and (2) local distribution of vegetational environment, the latter being uniform over the area of the plant community. Contiguous areas differing in physical and vegetational conditions will be expected to differ also in animal population, in a degree comparable to that of the differences in environmental conditions.

Physical habitats, and plant communities, sometimes alternate, sometimes intergrade; it is not unreasonable to expect accompanying alternation or intergradation of

[6] Differences in *species*, both plant and animal, are accompanied by differences in ecological constitution.

animal populations. Certain of the animal assemblages of sand habitats, as studied in central Illinois, intergrade; others, as oak forest and bunch-grass, differ radically.

The above considerations, if correct, appear to signify that, in ordinary climatic development of plant and animal life in temperate land environments, the area of the animal assemblage is that of the plant assemblage, both resting basically upon the physical environment. The plant and animal assemblages are therefore coextensive parts of a biotic association, composed of both plants and animals, and this association as a whole constitutes the real terrestrial community of living organisms.

B. Local Relations of Plant and Animal Assemblages (Relations Within the Association)

The more intimate relations between plants and animals are seen in the detailed study of a single association. The bunch-grass association of sand prairie is selected for illustration (*E:* 68).

1. *Similarity of Ecological Type of Plants and Animals.*—Shelford has shown (*A:* 593–594) that animals and plants may evince ecological similarity by similar response to the same general environmental conditions, behavior responses in animals[7] corresponding to structural responses in plants,[8] so that *mores* of the animal may be in accord with *growth-form* in the plant. Shelford states (*B:* 87) that "plants and animal communities are in full agreement when the growth-form of each stratum of the plant-community is correlated with the conditions selected by the animals of that stratum."

In the bunch-grass there is general agreement, according to this criterion. The herbaceous stratum is occupied mainly by tuft and mat plants—bunch-grasses, cactus and a few half-shrubs. Associated with the tuft or mat growth-form is the sedentary mores of the plant-inhabiting animals (leaf-beetles, stem-borers, ambush-bugs, etc.). A considerable proportion of ground surface

[7] Or motile organisms, cf. *C:* 305.

[8] Or sessile organisms.

is bare sand; in the interspaces between the dominant plants are slender annuals (interstitial plants), and here are also found animals of the roving mores of the ground stratum (interstitial animals). Many of these are swift-running and predaceous (six-lined lizard, tiger beetles, lycosid spiders).

Correspondence in ecological type of plants and animals in the bunch-grass is not complete in several respects. Shelford mentions types of disagreement (*B:* 88; *C:* 306–308), and there is a further important kind of disharmony, in mixed associations, due to presence of diverse types of plants and animals (*D:* 163). Mixed associations are quite frequent in forest border regions, and in the transition area between two provinces. The plant and animal assemblages of a given habitat, particularly if climatic and extensive, are usually in general ecological agreement, and the exceptions are likely to be infrequent or temporary (Shelford, *B:* 88).

2. *Relative Dependence of Plant and Animal Assemblages.*—There is evidence that the agreement of plant and animal assemblages of terrestrial associations is often a matter of accommodation on the part of the animal assemblage. In the early stages of development of vegetation, local physical conditions dominate; in later stages the vegetation assumes the type determined by climatic conditions, and exerts nearly complete control over local physical factors. In established associations, therefore, the locally dominating environmental feature is the vegetation. Shelford states that in the several associations of a successional series, the dominating animal mores are correlated with the dominating conditions (*B:* 94) and that, as the forest increases in density, the animals make use of the vegetation in increasing degree, particularly for breeding-places, and as places of abode (*B:* 90). Many grasshoppers of open grassland depend upon a particular kind of soil for egg-laying, while those of closed forest lay eggs in fallen logs—a condition of the plant environment (*D:* 163).

The sand-prairie vegetation is in an intermediate stage, certain animals depending chiefly on the presence of loose bare sand, others on the bunch-grass vegetation. With development of bunch-grass into closed grassland, the interstitial animals are eliminated. The animals of established associations, while in accord with climatic physical conditions, are perhaps more intimately affected by vegetation conditions. Since established associations are very much more extensive than primitive associations, the importance of vegetation as a dominating part of the environment for animals becomes apparent, and we may conclude that the character of the plant assemblage determines, to a large extent, the ecological type of the animal assemblage.

3. *Correspondence in Distribution within the Association.*—The uniformity of physical and vegetational conditions is only relative. There are spots in the bunch-grass association in which local invasion of blue grass has occurred, darkening and binding the soil. In such partly humified situations, small colonies of the corn-field ant, not occurring elsewhere in the bunch-grass (*E:* 57), have been found. There are also areas some few feet in diameter in which the bunches of grass are few, small and scattered. In these relatively bare patches the abundance of interstitial animals is greatly increased. More direct relations are seen in the case of animals associated with particular species of plants. Within the association, any animal species, like any plant species, may be distributed generally throughout the area, or it may be restricted to a part of the area characterized by a slight environmental difference, or it may occur in scattered parts of the association, characterized by scattered local differences (*D:* 168). There is evidence that, in so far as the vegetational environment is concerned, distribution of animals within the association is usually a direct function of similar distribution of plants.

4. *Uniformity of Species Composition of Plant and Animal Assemblages.*—It has been seen that plant assem-

blages of definite ecological type, as regards growth-form, etc., are regularly accompanied by animal assemblages of similar ecological type, as regards mores. Interest attaches also to the problem whether associated plant and animal assemblages show definite *species* relations.

One familiar with a certain association, who visits a representation of that same growth in a different part of the same climatic region, will be struck with the fact that a large proportion of both plant and animal species is well known, while a certain proportion, perhaps considerably smaller, is new to him. The writer has been impressed with the similarity of the plant and animal populations of the sandhills of central Nebraska and of eastern Colorado, to those of the sand prairie of central and western Illinois, despite the fact that certain species are not common to the two areas. Tiger-beetles, blow-snake, grasshoppers, box-turtle, six lined lizard, western meadow-lark, white-footed mouse, among the animals; prickly-pear, lead-plant, bunch-grasses, sand-bur, sand evening primrose, among the plants; are represented in the two areas either by the same or by closely related varieties and species. There are no yuccas or sand-sages in the Illinois sand prairie, no lizard *Holbrookia* nor lubber-grasshopper *Brachystola;* and there are certain eastern species not found in the western sandhills. But on the whole the species (particularly the important species) common to the two areas are more numerous. This is the more remarkable in view of the fact that distribution of sand prairie is discontinuous, the largest, nearly uninterrupted gap being several hundred miles in extent. Many of the animals, as well as plant species, of dry mixed prairie-grass in loamy soil, are the same along the mountain-front in Colorado (Vestal, 1914*b*) as in north-central Illinois. The likenesses become much more impressive as distance is decreased.

Absolute identity of species composition, where large numbers of species are involved, is an ideal condition,

never actually attained. No one can say just what proportion of species-in-common is necessary for two growths to be said to represent the same association. In addition to likenesses and differences of environment, of aspect, and of history, which must be weighed, the different plant and animal species vary so much in importance in the association, in physiological variation and in range of environmental tolerance, that associations can hardly be separated or placed together on a statistical basis. A comparison of species is fair if the following kinds of plants and animals are left out of consideration; (1) those of limited range within the climatic region or province, including species belonging more properly to other provinces; (2) those of very indefinite habitat-relations, which are found in nearly any kind of habitat; (3) those of special restricted habitats, which may be scattered about in many kinds of associations, as moist dead wood, in which particular fungi, beetles, perhaps snails, myriopods and pill-bugs, are usually found; or as excrement of grazing animals, in which certain molds, certain dipterous and scarabæid larvæ, etc., regularly occur, irrespective of surrounding conditions; (4) invaders from nearby associations; (5) ruderal and introduced species; and possibly one or two other groups. The second and third groups may be called the irregular element; the fourth and fifth may be known as the derived element. While these groups make a formidable list, their representatives constitute usually a very small proportion of the organisms of the association. The other organisms, and some of these, follow habitat-differences, as represented in different associations, very closely.

Since hardly any two species are identical in habitat-relations, geographic and even local variation must be looked for, but since many species resemble each other more or less closely in general ecological relations, there come to be recognized certain ecological groups of species, each characterized by a general type of growth-form in plants, or by a general kind of mores in animals, and

these groups may be considered to be small or large, according as we emphasize minor differences or general likenesses.

Now within any limited region (let us postulate first an area removed from the influence of an adjoining province) there are only a limited number of ecological groups, of growth-forms of plants, and of mores among animals, each group represented by a limited collection of species. Each habitat within this restricted area will be characterized by definite physical conditions, and with these will be correlated certain growth-forms of plants and certain mores of animals, each represented by as many of the species as can migrate into and survive within the area, as determined first by capabilities of migration and by habitat-selection, and second by interrelation of species and of individuals. It follows that physical complexes which are alike will become populated with similar complexes of ecological groups, represented by similar collections of plant and animal species, and that unlike physical areas will be occupied by different combinations of ecological groups, and will be composed of different species. Two areas within this region which have similar physical conditions and similar plant growths will be expected to have a large number of animal species in common, although direct relations between species of animals and species of plants obtain only rarely (between comparatively few associated plant-and-animal pairs). It is to be noted that species composition of the animal assemblage varies proportionately no more widely than does that of the plant assemblage.

No terrestrial continental region is sufficiently isolated to be free from influence of surrounding areas, and since the influences are different from different directions, and since there is continual change of physical conditions, and of range and abundance of plant and animal species, there must be more or less local and geographic variation of species composition within similar but separated habitats. Geographic variation is wider with distance.

because the geographic and physiographic complexes vary geographically, as well as the entire collection of plant and animal species which may invade the habitat. Within the area of the climatic province, however, or at least within the area of a subregion of the province, climatic, physiographic and biotic complexes are likely to be relatively constant, that is, likenesses of two areas are likely to be greater and more striking than differences. Within the province or subregion, therefore, it is to be expected that species composition of association of closely similar habitats will be relatively constant. Particular plant and animal assemblages will be found together, both associated with a particular habitat. Field observation bears out these expectations.

Conditions within the transition zone between two climatic regions or provinces are much more complex than in an area in the middle of a sub-region or province; climatic and physiographic conditions vary to wider extremes and are less stable; the total number of species near enough at hand to invade a given habitat is much greater. Mixed associations, often transitional as regards physical conditions, are composed of representatives of both provinces. Animals of a particular association of one province, may be found with plants of a similar or equivalent association of the other province. When *three* geographic elements are represented, as at the southern end of Lake Michigan (cf. *C*, and Vestal, 1914*a*), the complication of conditions is extreme. Even here, on the dry sand of old lake beaches, fairly typical representations of sand prairie can be seen; and though such habitats are shared with deciduous forest associations, and with associations of the northeastern coniferous forest province, and with mixed associations, the bunch-grass growth can still be recognized in dry shifting sterile sand, with bunch grass plant species, and bunch-grass animal species. The tendency towards uniformity of association of plant and animal assemblages is even here to be made out.

If the foregoing considerations relating to relations between plant and animal communities are correct, the thesis mentioned at the beginning of part V would seem to be justified, though the evidence is far from complete. Plant and animal assemblages are mutually interdependent; the plant assemblage dominates in established associations. Plant and animal assemblages correspond in geographic distribution, in distribution into communities, and in more detailed distribution within the habitat. They are made up of ecologically similar groups correlated with the same physical conditions or with each other. Though there are few direct relations between particular species of plants and animals, it so happens that within any restricted region, particular collections of animal species come into regular association with particular collections of plant species, the species composition within the habitat exhibiting a greater or less degree of uniformity, except for minor irregular and derived elements. The more restricted, or uniform in biological conditions, this region is, the greater the uniformity of the collection of species. Climatic and extensive associations, and established associations, show a greater degree of uniformity than local or primitive associations.

VI. SUMMARY AND CONCLUSIONS

The discussion is based principally upon the writer's study of prairie associations, the bunch-grass association of sand prairie in Illinois being chiefly used for illustration. Internal activities of the association are a complex of activities of all the organisms. Environmental influences are of three classes, physical, plant and animal. The characters of plants and animals are interpreted in their relation to these influences. Characters of plants may be classed as structural, physiological, biographical and numerical. Animals have, in addition, behavior or psychological characters. These groups of characters are intimately related, one to another. The relations of the animal to its animal-environment are of two kinds,

social and antagonistic, the latter relations being with food-species, competitors and enemies. Correlations of the various kinds of characters with relations involving food, competition and enemies, are given. According to its ecological constitution, each organism finds a status in the association, the whole being a self-contained and self-regulating system of activities.

Dependencies within the association are concerned mainly with sources and interchange of material and energy. Dominant plants (the most influential species) are those most intimately correlated with physical environment, as indicated by aggressiveness, abundance, frequence, size, etc. Dominant animals are most numerous among phytophagous forms. Dominance in an animal species includes dependence of other animals upon it (for food) plus the ability to thrive in spite of the drain upon its numbers. The degree of specialization of behavior is a convenient index of the relative influence of animals in the association. The dominant animals are moderately specialized, and carry on the ordinary work of the association. The highly specialized animals make use of space otherwise unoccupied, and food material not available to other species, or not taken by other forms. Least highly specialized animals act as a check upon undue departure from biotic equilibrium.

The association may be divided into minor groups of organisms, both in space and in time. Space-division is vertical, resulting in strata, and horizontal, resulting in sub-habitats of greater or less magnitude. The strata and sub-habitats present a larger or smaller degree of discontinuity and of internal variability. Time-distribution is diurnal, seasonal and annual. There are also time-variations produced by variability of weather conditions and by oscillatory disturbances.

The relations between plant and animal assemblages have long been known, in a general way, to be intimate. Plants and animals agree in similar response to common environmental influence, and in types of geographic dis-

tribution. Upon investigation, it begins to appear that plant and animal assemblages are coextensive parts of a biotic association, composed of both plants and animals, and this association as a whole constitutes the real terrestrial community of living organisms. Plant and animal assemblages are mutually interdependent; the plant assemblage dominates in established associations. Plant and animal assemblages correspond in geographic distribution, in distribution into communities, and in more detailed distribution within the habitat. They are made up of ecologically similar groups correlated with the same physical conditions or with each other. Though there are few direct relations between particular species of plants and animals, it so happens that within any restricted region, particular collections of animal species come into regular association with particular collections of plant species, the species composition within the habitat exhibiting a greater or less degree of uniformity, except for minor irrégular or derived elements. The more restricted in area, or uniform in biological conditions, this region is, the greater uniformity of the collection of species. Climatic and extensive associations show a higher degree of uniformity than local or primitive associations.

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SHORTER ARTICLES AND DISCUSSION

ANOTHER HYPOTHESIS TO ACCOUNT FOR DR. SWINGLE'S EXPERIMENTS WITH CITRUS

THE results of the cross-breeding experiments with forms of *Citrus* by Walter Swingle have given rise to quite a number of different hypotheses, to account for the facts observed.

The facts are simply these. All the different forms of *Citrus* used in the experiments, *Citrus trifoliata,* the lemon, orange and other citrous fruits have, so far, proved to reproduce their own type through seed.

Nevertheless, the plants raised from one single cross are exceedingly different among themselves. And yet, all these new forms, for so far as tested, have proved truly to reproduce their own kind only, if sown.

The theories offered to account for these facts are rather complex. So far, we have not seen the simple hypothesis which we want to add to the others.

The fact, that the F_1 from almost every cross between types of *Citrus* is multiform, can only be accounted for on the assumption, that the parent plants are impure (heterozygous) for a number of genes. The difficult question is this: how can a tree, impure for a number of genes, produce seed which always only reproduces the type? We know, that if a plant reproduces itself by an asexual method, all its daughter plants are pure for those genes in respect to which it was pure, impure for those genes for which it was impure. Is it possible that in these trees the seeds normally produced are not derived from a union between two normal gametes? In *Citrus*, with its adventitious embryos, this is very well possible. If the forms of *Citrus* used by Dr. Swingle are self-sterile, the seeds normally produced by these trees, are not produced by the union of two gametes, but as buds, asexually.

This hypothesis, that the *Citrus* used are self-sterile, and that the seeds normally produced, are produced asexually, fully accounts for all the facts. All the daughter plants from uncrossed seeds are genotypically identical with the mother plant, as in all clones. On pollenization by another tree, normal seeds are produced, each the result of the union of two real gametes.

These seeds contain different combinations of the genes, for which the parent plants are impure, as normally. The F_1 generation for this reason becomes as diverse as such generations always are, if the parents are impure for numerous genes.

But these daughter plants, although impure for a number of genes, can, because of their self-sterility, in their turn only produce seed asexually and therefore their offspring will be like themselves.

It should not be difficult to test our hypothesis. It seems easier to find out, whether the seeds produced without crossing in *Citrus* contain the embryo formed by fertilization of the embryo sac, or embryos formed adventitiously by the adjacent tissue, than to test any of the other theories, which assume a peculiar behavior of the chromosomes.

Our hypothesis, that a variable F_1, of only true-breeding plants (from the union of two true-breeding forms), results from habitual self-sterility and asexual production of seed, with real fertilization in the case of a cross taking place, not only accounts for the facts found by Swingle, but also for those found by Rosen with *Erophila verna*. These facts were somewhat different. The F_1 plants were all identical, and somewhat intermediate. They gave rise to a variable F_2 generation of which all the plants bred true to their type. These facts can be explained on the assumption, that *Erophila verna* is self-sterile, and that, in the absence of cross-fertilization, unfertilized egg-cells develop parthenogenetically. Such F_1 plants, which are impure for a number of genes, should therefore produce as many different kinds of F_2 plants, as there are female gametes produced, and in the same proportions. In the case of such a plant being impure for two genes, we should expect it to produce plants of the four different types, not in the usual proportion of 9 : 3 : 3 : 1, but in equal proportions, 1 : 1 : 1 : 1. The F_2 plants from such seed could only be pure for all the genes present.

It would be possible in *Erophila verna* to find out whether F_1 plants, impure for two genes, produced daughter plants of the four kinds, *AB*, *Ab*, *aB*, and *ab*, in the proportion of 9 : 3 : 3 : 1, or in proportion 1 : 1 : 1 : 1, and thus to test our hypothesis.

To find out, whether it is possible, that a plant, impure for a number of genes, produces a variable F_2 generation of only completely homozygous plants, we have begun a series of experiments with squashes. Some hybrid plants have not produced a

single fruit from carefully sealed female buds, others have given plenty of empty fruit, but some hybrids have produced several fruits, full of viable seed. If this seed is formed by the parthenogenetic development of unfertilized normal egg-cells, as we have reason to believe, we expect to raise a variable F_2 generation of exclusively homozygous plants. If these seeds have developed by apogamy, or any other asexual process, we expect to obtain a second generation consisting exclusively of plants like the original hybrids. Thus we will have a non-cytological test to decide between apogamy and true parthenogenesis.

A. C. Hagedoorn,
A. L. Hagedoorn

Bussum, Holland,
March 18, 1914

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THE

AMERICAN NATURALIST

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MULTIPLE ALLELOMORPHS IN MICE

PROFESSOR T. H. MORGAN

COLUMBIA UNIVERSITY

SOME breeding experiments with mice that I have been carrying on during the last two years have shown that yellow, gray gray-belly, gray white-belly and black are allelomorphs. To this series a fifth allelomorph may possibly be added which for the present may be called new gray. This quadruple (or quintuple) system of allelomorphs fulfils the conditions of a multiple series in that only two of the allelomorphs can exist at the same time in any individual. In other words, a mouse may be pure for any of these genes (except for yellow, in which the pure form is not viable), or a mouse may be heterozygous in any two of the genes, but never in more than two. The evidence that establishes this series of allelomorphs may be briefly stated as follows:

In 1911, I pointed out that if yellow mice (producing yellow and chocolates) are bred to agoutis (grays), and their yellow offspring mated, they should produce not only yellow and agoutis (as they did) but some chocolates (or blacks) also; but no chocolates appeared. I stated that the results obtained were explicable if yellow and agouti are allelomorphs.[1]

[1] The discussion in the same paper of the presence of chocolate yellow and black bars in the ticked hair in relation to the occurrence of chocolate, yellow and black color in domesticated races may only confuse the ontogenetic production of characters with the gametic inheritance of factors. The

Sturtevant (1912) showed that the results are also consistent with the hypothesis that there is close or complete linkage (genetic coupling) between yellow and agouti. In principle this is the same as saying that when yellow and agouti enter from different sides (mother and father) they separate in gametogenesis, or in other words they "repel" each other and behave, as I said, like allelomorphs.

The numerical results would be the same whether yellow and agouti are treated as though completely linked or whether they are treated as allelomorphic. What I had vaguely seen in my 1911 paper was clearly explained in the following year by Sturtevant's treatment of the same data, to which he added that of Little and Miss Durham.

Sturtevant showed, from an analysis of Miss Durham's results, in which she used ordinary gray (gray "gray-belly") mice, that her results are consistent with the hypothesis of absolute linkage, or, on my interpretation, with the hypothesis of allelomorphism. Sturtevant's conclusions were promptly contradicted by C. C. Little on the evidence furnished by some of his earlier experiments, in which he obtained yellow, grays and black (or chocolates) in offspring from yellow to black (or chocolates). Such a result would be inconsistent with Sturtevant's hypothesis. Little also appealed to certain experiments of Miss Durham, in which, he stated, results like his own are given. Since Little has been unable to get again his former results, but has obtained evidence in favor of Sturtevant's view, and since it is clear that he misunderstood Miss Durham's evidence, his contradiction ceases to have any weight.

factorial hypothesis relates to those differentials that serve to separate different types in inheritance and is not concerned with the problem as to how those differentials produce their effects. Breeding experiments show that gray differs from black by one differential, from yellow by another, and from cinnamon by a third. So far as Mendelian segregation of these differential genes is concerned it is of no consequence that the gray hair is made up of a black, a yellow, and a chocolate band.

After the publication of my own and of Sturtevant's paper I set to work to obtain crucial evidence in favor of, or opposed to, the view that yellow and gray are allelomorphic. Little, also, it appears, has carried out some new experiments which he has recently published, with the results just stated. My own data have been ready for some time, but I have withheld them in order to get a sufficient body of evidence to make the case convincing, especially in the light of the possibility that the crossing over might occur in one sex and not in the other. For, if no crossing over occurred in the male, there might be crossing over in the other sex, which would not reveal itself unless the experiments were deliberately planned so that both sexes are tested. This consideration seems to have been overlooked by Little, for he has omitted in his confirmatory paper to give the sexes of the animals used. Without a knowledge of this relation even his confirmation fails to confirm (as he supposes) the view that he formerly combated.

Since Miss Durham worked with common gray and I with gray white-belly, and both are "repelled" by yellow, *i. e.*, both are allelomorphs of yellow, it follows that these two grays are also allelomorphic to each other.

The evidence that black belongs to the same series of allelomorphs is obtained in the following way: If a given yellow is mated to black, and yellow and gray offspring are obtained, and if then the yellow offspring are mated to black again and now give yellow and black only, the proof is furnished; for in the first mating yellow and agouti have repelled each other, and the yellow-bearing gametes have united with the black gametes of the other sex to give the yellow offspring. The second mating shows that black is now repelled in turn by yellow and is therefore allelomorphic.

This may be illustrated in the following way: Let B^Y = yellow, b = black and B = gray. These three factors may be treated as allelomorphs, then:

Yellow B^YB by black bb.

Gametes of P_1 yellow B^Y–B.
Gametes of P_1 black b–b.

F_1 B^Yb = yellow.
Bb = gray.

Gametes of F_1 yellow B^Y–b.
Gametes of pure black b–b.

F_2 B^Yb = yellow.
bb = black.

But if yellow and black and gray are not allelomorphic the same matings should give the following results:

Y' = yellow. y' = not yellow. b = black. B = "gray" (not black).

Yellow $Y'y'BB$ by black $y'y'bb$.

Gametes of P_1 yellow $Y'B$–$y'B$.
Gametes of P_1 pure black $y'b$–$y'b$.

F_1 $Y'B\ y'b$ = yellow.
$y'B\ y'b$ = gray.

Gametes of F_1 yellow $Y'b$–$Y'B$–$y'b$–$y'B$.
Gametes of pure black $y'b$–$y'b$.

F_2
$Y'b\ y'b$ = yellow.
$Y'B\ y'b$ = yellow.
$y'b\ y'b$ = black.
$y'B\ y'b$ = gray.

On the second assumption yellow, gray and black should appear in the back cross. The former and not the latter view is therefore consistent with the actual results.

The Symbols Employed

It is, of course, a matter of secondary importance what system of symbols is followed. The requirements are simplicity, consistency and suggestiveness, but one can not always arrange to have all three at the same time. The simplest scheme, for a system of allelomorphs like these, would be to have some common letter to indicate their relation and an exponent to suggest the different characters for which each stands. If we take the symbol b (black) for the common letter, and use capitals for dominance, the allelomorphs will be:

b = black.
B^G = gray gray belly.
B^W = gray white belly.
B^Y = yellow.

If one preferred to take Y (yellow) as the common letter the series would be y'^b, y'^g, y'^W, Y'; or, if one preferred

to take G (gray), as the common letter, the series would be g^b, g^W, G, g^Y. On the whole the first series seems to me somewhat preferable.

The factor for cinnamon is entirely independent in heredity of the preceding series of allelomorphs. This factor may be represented by *ci* and its normal allelomorph by *Ci*. The formula for the wild gray would then be *Ci Ci*, and that for cinnamon would be *ci ci*. Black would be *b b*, and the double recessive cinnamon black (or chocolate) would be *bb ci ci*. Chocolate is one of the commonest types of domesticated mice and since I have used it very extensively in my matings, its relation to the other types may be further stated. It is known that if chocolate is bred to wild gray, and if the gray offspring that are obtained are then inbred, they give, in F_2, the following classes: 9 wild gray, 3 cinnamon, 3 black, 1 chocolate.

It is clear that chocolate is the double recessive type. Of the two genes, that differentiate chocolate from wild gray, chocolate has one in common with cinnamon and the other with black. In other words, chocolate is cinnamon black, and technically should receive this name.

The Experimental Evidence

Is There a Separate Factor for White-belly?

The first series of experiments was made in order to determine whether the peculiarity of white-belly, shown by the wild race of white-bellied grays, is due to a factor that may be separated from the gray white-bellied mice, or whether it is completely linked to gray (or allelomorphic to it). As wild gray house mice offer some drawbacks in breeding work, I used cinnamon blacks (chocolates). Gray white-bellied mice were bred to

[2] It is not possible to make a system of allelomorphs (in which the "compounds" are serially epistate to each other) consistent entirely with the system of nomenclature that I have suggested for the usual cases in which mutant allelomorphs are contrasted with the normal allelomorphs of the wild (or supposed original) type.

chocolates.[3] The gray white-bellied offspring were selected and these were bred again to chocolate. The cross, in regard to sex, was made both ways. If there is an independent factor for white-belly that can separate from the factor for gray gray-belly, then some gray gray-bellied mice should appear. None were obtained, as the following table shows. We must conclude either that there is one factor that gives the gray white-bellied coat, or else that the postulated factor for white-belly is so closely linked to the gray factor that it has not separated once in 100 times. Therefore unless such a separation occurs it is simpler to assume one factor for gray white-belly that is allelomorphic to black and to gray gray-belly, etc.

TABLE I

Mating	Gray or Cinnamon White-belly		Black		Chocolate		White	
	♂	♀	♂	♀	♂	♀	♂	♀
Gwb ♀ by Ch ♂....	7	21	2	9	5	11	3	1
Ch ♀ by Gwb ♂....	2	14	3	10	4	10		
Totals..............	9	35	5	19	9	21	3	1

Taking both crosses together, there are 44 grays to 54 blacks and chocolates, which approximate at least to expectation. To these numbers I may add the following data taken from similar experiments made for other purposes in which one parent was, as before, gray white-belly.

Gray-white Belly.		Black or Chocolate.	
♂	♀	♂	♀
17	25	20	20

Presumably, therefore, the results may be treated as though a single gene for gray white-belly exists. It will be observed that the experiment has been made in two ways, for at the time I was aware of the possibility that crossing over, if it occured, might be limited to one sex.

[3] At the time when the experiment was made all the gray white-bellied mice were heterozygous for black and for agouti (including some with the factor for cinnamon).

We are justified, therefore, in treating gray white-belly as an allelomorph of gray gray-belly, the former dominating. If crossing over should occur, it might perhaps only be realized in the gray or cinnamon mice, since it is possible that the ticked condition of the hair (that is, common to gray and to cinnamon) is necessary to realize this condition. The expected crossover that would be observed would be gray gray-belly mice. The contrary class would then be black or chocolate mice that carry the factor for white-belly that might or might not show the influence of the supposedly separable factor.

My white-bellied stock of mice had been killed after my earlier results had been published, but Mr. B. B. Horton had kept some of my original stock alive, and from him I obtained a few of these mice in 1912 to carry on the above experiments.

An extraordinary sex ratio appears in the next to the last table, where there were 26 males to 76 females, approximately 1:3. The mice were entered when about three weeks old. The sex was noted, but no special attention given to the determination. There is some chance of mistaking the sex of young mice, but one familiar with these animals can determine with certainty the sex at three weeks if sufficient care is taken. I have no reason to suppose that I made such errors which would have to be frequent to give these results. If taken, then, at their face value, the data seem to show that there is a sex-linked lethal gene present here. It is not linked to any of the factors involved, and this is not expected, since neither black nor agouti is sex-linked. If further work confirms this conclusion (and I hold it as a provisional conclusion until it can be further studied) we have here the first evidence of a sex-linked gene in mice. A sex-linked lethal should give a sex ratio of 1♂:2♀.

The Allelomorphism of Yellow, Gray and Black

The allelomorphism or "repulsion" of yellow and agouti (gray) may be tested in various ways. One of the

simplest tests is the following: Yellows were bred to chocolates. The combination gave yellow and agouti offspring, when certain yellows are used, and yellow and chocolate offspring when other yellows are used. Mixed litters of yellow, agouti and chocolate do not appear. Now when yellow and agouti appear in a given litter (as above) the yellow parent must have carried agouti. If her yellow gene "repels" the agouti gene, then none of the yellow daughters should contain agouti genes, consequently if such yellows are next bred to chocolate the offspring should be only yellow and chocolate (or black) and never yellow and agouti. This, in fact, is what my experiments have shown. In the two following tables the results of crossing yellows by chocolates are given by litters. The yellows that were used at first were for the most part heterozygous for gray white-belly, hence in the earlier litters yellows and grays were generally obtained. The yellow offspring of these earlier litters were for the most part used in the later experiments, hence the later litters are made up of yellows and chocolates. The records (not given here) showed in every case that yellow mice from litters of yellow and gray gave, when bred to chocolate, only yellows and chocolates.

TABLE II

YELLOW ♂ BY CHOCOLATE ♀

LITTERS

Yellow	1	1	1	4	3	1	3	2	4	4	9[4]	4	4	2	5	5	4	3	5	7	2	2	2	2	3	4	3	2	4	1	2	2	2
Gray	.	2	.	5	4	2	2	.	.	4	4	5	5	.	.	3	4	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.
Chocolate	.	.	1	.	.	.	.	.	4	.	. .	.	.	4	.	.	.	2	3	4	3	.	3	3	.	2	3	2	.	3	4	2	3
White	1	.	.	.	.	.	.	2	.	.	. .	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

TABLE III

YELLOW ♀ BY CHOCOLATE ♂

LITTERS

Yellow	4	1	4	4	3	4	4	2	4	1	4	8	8	1	2	2	8	3	2	2	1	1	4	3	4
Gray	5	..	2	5	2	1	1	2	..	3	5	1	3	1	..	..	3	..	..	..	..	..	..	..	..
Chocolate	..	..	..	..	..	..	..	..	1	..	..	..	..	..	2	2	..	1	..	2	3	4	2	3	1
Black	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2
White	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	2	..	..	..	..	..	..	..	..	..

[4] Probably two litters combined.

TABLE IV

SUMMARY OF LITTERS

Yellow and Gray		Yellow and Chocolate	
Yel.	Gray	Yel.	Choc.
101	78	70	67

The experiment is not demonstrative, however, unless both the yellow daughters and sons are bred to chocolate, for it might be that yellow and agouti are linked and crossing over might occur in one sex and not in the other sex. For instance, if we start again with yellow by chocolate, then if their yellow offspring contain agouti linked to yellow that does not cross over in one sex, let us say in the males, it follows that a yellow male bred to chocolate would give only yellows and chocolates, for the agouti gene would go with the yellow. Therefore, both sexes must be tested. This essential element in the proof has been overlooked by Little, for he fails to state whether his test experiments were made with both sexes. In my main experiments I have used yellow sons only, and the tables are based on those data, but in a few cases I have mated the yellow daughters (whose brothers were agouti) also to chocolate and have found that these females give only yellows and chocolates, which shows for both sexes that no crossing over of yellow and agouti occurs.

A specific case will illustrate this point. A yellow male was bred to a chocolate female and gave 5 yellow and 7 gray offspring in two litters. One of the yellow daughters was bred to chocolate and in four litters produced 11 yellows and 9 chocolates. A yellow granddaughter gave 9 yellows, 7 chocolates and 4 whites.

A yellow female bred to chocolate gave 8 yellows and 16 chocolates, but as I have no record of the preceding generation, I can not be sure that this result is comparable to the last. It shows at least that a yellow female gave only two kinds of offspring.

A "New Gray" Factor

A word may be added about the "new gray." In the original stock obtained from Mr. Horton there was a

gray female with a not-pure-white belly. She was not used in the main lines of the experiments described above. But she was kept in stock and bred with chocolates. About a year later I noticed in the offspring of a pair of cinnamon white-bellied mice a few mice that looked like chocolates, but which showed, on closer inspection, distinctly ticked hair. One of these new grays bred to black (heterozygous) gave some chocolates, blacks, new grays, and one very dark, almost black, mouse with ticked hair.[5] The female was bred next time to a house mouse (gray gray-belly) and produced all gray gray-bellied offspring that had a dark coat, but not nearly so dark as that present when the new gray is heterozygous for black. Until further tests have been made it can not be stated whether or not the new factor belongs to the yellow-black system of quadruple allelomorphs.

[5] The resemblance of this mouse to the rabbit "agouti-black" homozygous for black is very striking (Punnett, *Jour. of Genetics*, II, 1912).

THIRTEEN YEARS OF WHEAT SELECTION

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Introduction

In 1901 the Minnesota Agricultural Experiment Station planted a number of varieties of wheat from the *polonicum, spelta, turgidum, durum* and *vulgare* types in foundation beds in order to have specimens of these different types always on hand for class work, hybridization or demonstration purposes. Six of these varieties—hedgrow (*turgidum*), Russian (*vulgare*), common speltz (*spelta*), kamouka (*durum*), and Polish (1) and Polish (2) (varieties of *polonicum*)—have been grown continuously since that time and an effort has been made to improve them by selection. The method followed was that introduced at this station by Professor W. M. Hays and called the "centgener" method.

The centgener method consists, briefly, in starting with individual plants, planting one hundred selected kernels from each plant at equal depths and at equal distances apart in separate plots. A plot of one hundred plants is called a centgener. Careful notes are taken on the plants in each centgener and at harvest time five or more of the highest yielding plants are selected from which the seeds for planting the next year are taken. From these five best plants from five to ten of the best heads are selected and thrashed together. One hundred of the largest and plumpest kernels are then selected out of the seed obtained by thrashing these selected heads, and these are planted in the centgener test the next year. This work is continued from year to year, each season the hundred best kernels from the five or more best plants being planted in succeeding centgeners.

In 1908 an experiment was planned with the object of developing a strain of wheat which would have a minimum amount of culm exposed between the base of the spike and the upper leaf sheath, or in other words, to produce a short-necked variety of wheat. The ultimate purpose of reducing the neck lengths was to reduce the area of the stem exposed to the black stem rust. Since this rust ordinarily does little damage to that portion of the culm enclosed in the leaf sheath, it was thought that a short-necked wheat would be more likely to escape serious damage from stem rust than a long-necked kind. For this work individual plants were selected which had short necks and the seed from these were planted in separate centgeners. Each year at harvest time ten or more plants which appeared to the observer to have the shortest necks were selected from each centgener and measurements of their neck lengths were made and recorded. One hundred kernels were saved from these shortest necked plants each season for subsequent centgeners, thus making a continuous selection for short neck lengths.

The data derived from the above experiments seems to throw some light upon the much-discussed question as to whether or not selection within a pure line can increase yield or change type enough to make it a desirable practise from the practical breeder's standpoint. In both of the experiments, we have the requirements for a pure line satisfied. Wheat is a normally self-fertilized plant. Each centgener was started from a single head in 1901 and these heads have bred true to type ever since.

The long period of years over which this experiment has extended makes the data particularly valuable. One of the adverse criticisms to most pure line work is that it has not extended over a long enough period of time. Thirteen years are about as long as any practical breeder would be apt to keep up selection on one pure line and covers the longest period of continuous selection for a self-fertilized plant yet reported.

Another criticism to pure line investigations is that in

many cases it has not appeared certain that the material studied was a pure line. Since the plants have bred true to type throughout the whole period of study, it is obvious that this criticism will not hold for the data herein presented.

The work has been conducted at this station under the direction of Professor W. M. Hays from 1901 to 1905, under Professor E. C. Parker 1905 to 1908, under Professor Andrew Boss from 1908 to 1911 and under Professor C. P. Bull 1911 to 1913.

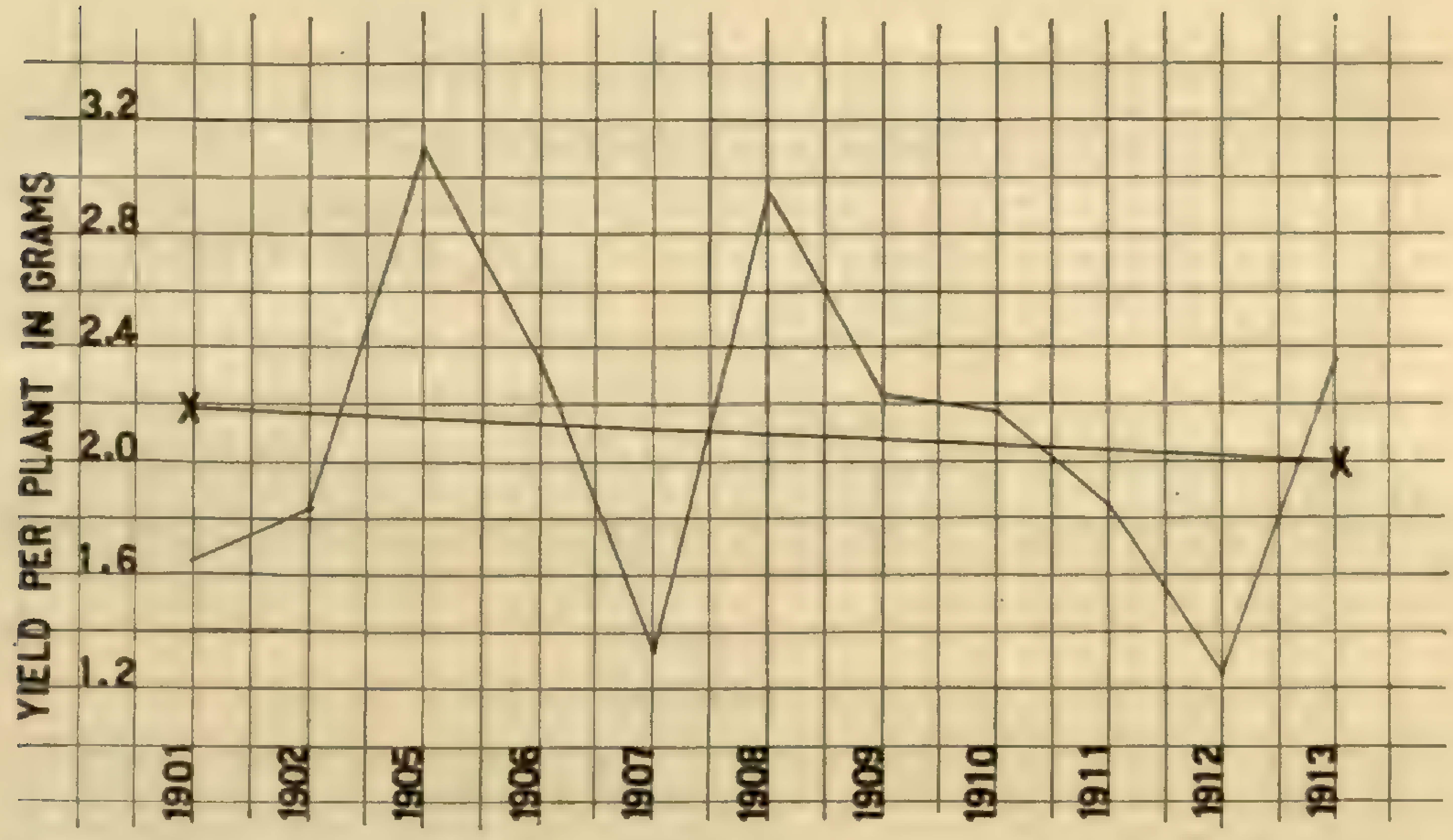


PLATE I. Average yield per plant for all varieties. X–X, fitted straight line.

SELECTION TO INCREASE YIELD

The varieties studied, the average annual yield of each variety and the average yield per plant for the six varieties under test are shown in Table I. In the years 1903 and 1904 weather conditions were unfavorable, making it impracticable to obtain correct average yields per plant, so data for these years were omitted. However, selections of the best plants were made in these two seasons as in the others and the best seed from them were kept for planting, so the continuous selection for increased yield was uninterrupted.

TABLE I

SHOWING YIELD PER PLANT—YEARS 1901–1913

Name of Variety	Yield per Plant in Grs.										
	1901	1902	1905	1906	1907	1908	1909	1910	1911	1912	1913
Hedgrow	3.10	2.80	3.69	2.48	1.27	3.75	2.49	2.55	2.02	.99	3.67
Russian	1.00	1.70	3.57	1.96	1.71	2.74	2.71	2.17	1.95	1.37	2.70
Speltz	2.40	1.80	3.99	2.99	1.38	3.38	2.40	2.86	2.01	2.14	2.59
Kamouka	1.50	2.50	1.99	2.69	1.39	3.31	2.19	2.48	1.67	1.35	2.16
Polish (1)	.80	1.30	2.52	2.04	1.03	1.48	1.91	1.70	1.56	1.12	1.74
Polish (2)	1.10	.95	2.83	1.97	1.26	....	1.61	1.31	1.78	.51	1.33
Average	1.65	1.84	3.10	2.35	1.34	2.93	2.22	2.18	1.83	1.24	2.36

SELECTION TO INCREASE HEIGHT

The average height of the plants for each year of the test is shown in Table II. Though no attempt was made to select for increased height, since a number of workers have shown that height in the small grains is distinctly correlated with yield, it is natural to suppose that the selected plants were among the tallest as well as being the highest yielders of each year's crop. When this experiment was begun, it was not known that height and yield

TABLE II

SHOWING AVERAGE HEIGHT PER PLANT—1901–1913

Name of Variety	Height in Inches									
	1901	1902	1905	1906	1908	1909	1910	1911	1912	1913
Hedgrow	36	41	42	43	46	41	38	41	36	36
Russian	34	37	40	35	44	41	33	36	35	32
Speltz	34	38	37	47	44	41	39	42	39	35
Kamouka	36	34	34	38	40	40	32	38	36	33
Polish (1)	40	38	41	38	42	42	33	39	38	33
Polish (2)	28	30	37	37	.....	35	31	38	31	32
Average	35	36	38	39	43	40	34	39	36	33

were correlated, so the figures on height were kept merely as a matter of general interest and with no idea that they would have bearing on the problem. Among those who later found height correlated with yield are Deneumostier ('10),[1] Love ('11),[2] Myers ('12),[3] Leighty ('12)[4] and

[1] Deneumostier, C., "Correlations in Wheat," *Ann. Gembloux*, 20, No. 5, 1910.

Selection to Decrease Neck-Lengths

The result of the selection for short neck-lengths is shown in Table III. This is a clear illustration of how misleading short-term experiments may be. Had the experiment been discontinued at the end of the third year, the figures would have indicated that it was possible to modify this character very rapidly by selection. However, in the following two years the neck-lengths seemed to revert to the mean of the pure lines, and the last year they were actually longer than when the experiment was started. The reduction in the first three years was probably due to growing conditions.

TABLE III

Showing Result of Selection for Short Necks

	Average Neck L ngth in Curve				
	1909	1910	1911	1912	1913
Series *A*	7.4	1.86	.24	7.34	9.54
Series *B*	6.1	1.12	.79	8.13	11.6
Series *C*	5.8	1.65	.56	7.53	8.21
Series *D*	5.2	2.08	.59	10.47	13.82

Discussion

From the data presented in these tables, it is evident that there has been no permanent gain for these thirteen years of selection either in yield per plant, height of plant, or shortening of neck-lengths. The expected seasonal variations occur. A comparison of the yield of Haynes Blue Stem, which is grown extensively in Minnesota, and was continued in the variety test without any attempt at selection throughout the whole period, with Hutcheson ('13).[5]

[2] Love, H. H., "A Study of the Large and Small Grain Question," *An. Rep. Am. Br. Asso.*, 7: 109–118, 1911.

[3] Myers, C. H., "Variation, Correlation and Inheritance of Characters of Wheat and Peas," Cornell University Thesis, 1912.

[4] Hutcheson, T. B., "Correlated Characters in *Avena sativa*, with Special Reference to Size of Seed Planted," Cornell University Thesis, 1913.

[5] Leighty, C. E., "Studies in Variation and Correlation of Oats, *Avena sativa*," Cornell University Thesis, 1912.

the average yield of the selected varieties, is shown in Table IV. The average yield in bushels of the Haynes Blue Stem is also platted in comparison with the average yield of the selected varieties in Plate II. In 1912 a severe hail storm injured the variety plats so much that

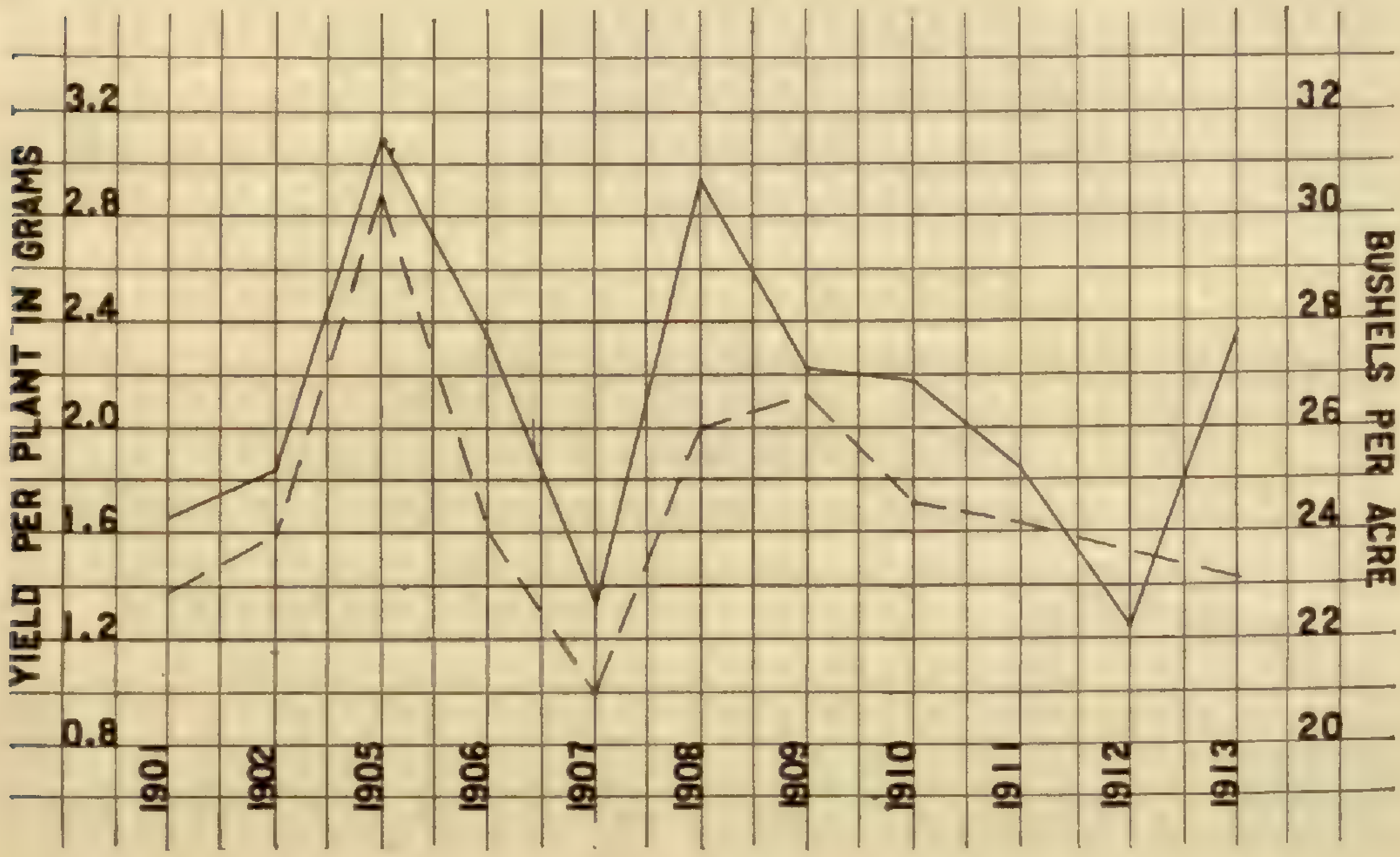


PLATE II. Comparing seasonal fluctuations in selected lines with unselected Blue Stem. Solid line, yield per plant in grams for selected lines; dashed line, yield in bushels per acre for Blue Stem.

it was thought best not to include the yield of the Haynes Blue Stem for that year. This gives an incorrect appearance to the curve, as it was extended just as if this year was present and midway between 1911 and 1913 in yield. It will be noticed from Table IV and Plate II that the

TABLE IV

COMPARING SEASONAL FLUCTUATIONS IN SELECTED LINES WITH UNSELECTED BLUE STEM

	1901	1902	1905	1906	1907	1908	1909	1910	1911	1912	1913
Yield in grs. per plant for selected lines..........	1.65	1.84	3.10	2.35	1.34	2.93	2.22	2.18	1.83	1.24	2.36
Yield in bu. per acre for blue stem..........	22.9	23.9	30.4	24.00	21.00	26.00	26.6	24.6	24.2	.....	23.2

fluctuations from year to year agree very closely. These data indicate that increased yield is due to favorable environmental factors and not to improvement by selection.

A comparison of the yield of each variety for the first five years of the test with that of the last five years is shown in Table V. The data in this table show that there is no significant difference in yield for these two periods. In Russian and Polish (1) there is a slight increase in favor of the latter period, but in the other four varieties there is just as much decrease for this period. However, there is not enough difference in any case to indicate either permanent improvement or decrease in yield. As far as these varieties are concerned, it seems that selection has brought about no permanent improvement.

TABLE V

COMPARING THE YIELD OF THE FIRST-YEAR PERIOD WITH THAT OF THE LAST FIVE-YEAR PERIOD

Name of Variety	1st 5-year Period		Last 5-year Period	
	Height	Yield	Height	Yield
Hedgrow	41.6	2.67	38.4	2.34
Russian	38.0	1.99	35.4	2.18
Speltz	40.0	2.51	39.2	2.40
Kamouka	36.4	2.01	35.8	1.97
Polish (1)	39.8	1.54	37.4	1.61
Polish (2)	33.4	1.62	33.4	1.31
Average	38.2	2.06	36.5	1.97

A curve of the yields of the six varieties under consideration for the thirteen years of the test was plotted and a straight line was fitted to it, by the method of the least squares, to indicate the trend of the yield. This curve is shown in Plate I. There is a slight downward tendency in this straight line, but it is not enough to indicate a tendency toward decrease in yield. The line fitted to the curve of height (Plate III) also shows a slight tendency downward.

The data herein cited are not sufficient for definite con-

clusions. However, the indications are that from a practical breeder's standpoint permanent improvement in pure lines in small grains, if possible, is certainly not rapid or apt to be very marked. Thirteen years of selec-

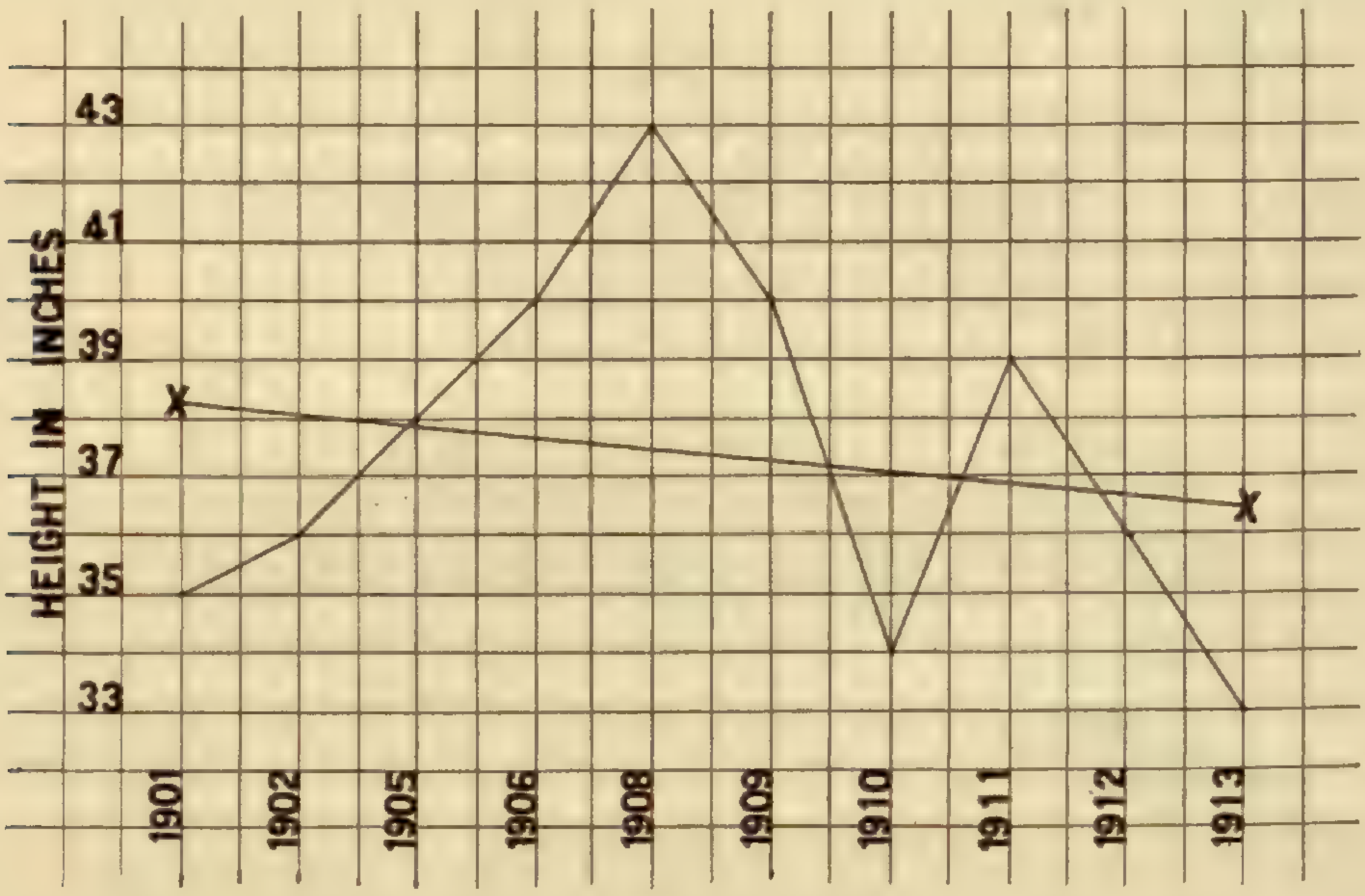


PLATE III. Average height of all varieties. X–X, fitted straight line.

tion covers considerable time and expense, and, as far as can be seen from the varieties reported in this paper, it has resulted in no permanent improvement. This would suggest that some other line of improvement must be sought. It is probable that much more rapid progress could be made by segregating pure lines from mixed populations and combining the desirable characters of these lines by hybridization.

PATTERN DEVELOPMENT IN MAMMALS AND BIRDS

II

GLOVER M. ALLEN

Boston Society of Natural History

Partial Albinism in Wild Mammals

Partially albinistic individuals of species that normally are wholly pigmented, occur frequently in a wild state, and almost any large series of a given species may contain a few. I have examined many such, in which it was perfectly evident that the white mark was due to areal restriction of some one or more of the primary pigment areas just as described in the various domestic species. It is apparent that the white markings in both are quite comparable, but in species under domestication no agency seems present whereby such pied individuals are eliminated, whereas in a wild state the sudden acquisition of a large amount of white in an individual would not only render him too different from his fellows, but might put him at a disadvantage because of a conspicuousness to which as a species he had not yet become accustomed.

There are many other species in which, as we now see them, white markings form a permanent and normal part of the pattern. Among those in which these white markings are few or simple, it is often evident that they are merely primary breaks between the pigment patches that have become more or less fixed by long periods of selection, whether natural, sexual or otherwise. As I shall endeavor to show, there are species in which a beginning has already been made towards the development of a pied pattern, though it has not yet become well fixed. Still other species show a more complicated white and pigmented pattern, the white portions of which can not readily be derived from primary breaks alone. Such I take to be highly developed patterns and make no attempt

to analyze them here. Examples of this type are seen in the zebra, the spotted skunks (*Spilogale*), the striped weasel (*Ictonyx*). Probably more than one factor is responsible for some of the combinations of stripes and spots seen, for example, in certain spermophiles (*Citellus 13-lineatus*), but I shall not now attempt a discussion of these.

One of the most frequent manifestations of pigment reduction in mammals is the presence of a white spot in the normally pigmented forehead. This is due primarily to the reduction of the ear patches, which fail to meet at their median edges. Perhaps, too, the apparent loss of the crown patch in some mammals still further tends to lessen the amount of pigment production at this point. Rabbits and hares very often have more or less white in the forehead, but none of the species has developed this sufficiently to make it a permanent mark. Moseley in his "Naturalist on the *Challenger*," speaks of a "black variety" of wild rabbit—doubtless introduced—"with a white spot on the forehead" as occasionally found on Teneriffe, Canary Islands, but this mark is common, and I have seen it in such widely sundered species as the eastern varying hare of New Hampshire and the black-necked hare native to Java. A specimen of Leisler's bat (*Nyctalus leisleri*) in the Museum of Comparative Zoology has a white spot in the middle of the forehead and another on the mid-ventral line of the abdomen—the first a primary break between the ear centers, the second probably a ventral primary break between those of the sides. Among the Insectivora, the West Indian *Solenodon paradoxus* has a white patch at the nape of the neck which has become a permanent part of its pattern. It is clearly the enlargement of a primary break separating the ear patches and neck patches on the median dorsal line. It is a fact of much interest that in a considerable series of this species in the collection of the Museum of Comparative Zoology hardly two have it developed alike, but it varies from a few white hairs to

a large patch 15 × 10 mm. wide. Evidently it has not yet become precisely defined in its limits, though now a permanent mark of the species.

White marks in the forehead are common among the species of the Mustelidæ or weasel family. A narrow white median line is present in the Javan mydaus and in the skunks (*Mephitis*) as part of the permanent pattern. In the badger (*Taxidea*) a white line is not only present on the forehead, but it is often extended medially so as to separate the pigment patches of both sides of the body. In the New York weasel (*Mustela noveboracensis*) of the eastern United States a few white hairs are often present on the forehead, and other instances could be multiplied. Among monkeys, a white spot on the nose is present in some species of *Lasiopyga,* and in an allied genus *Rhinostigma,* it is elongated vertically to form a white streak.

A yet more illuminating case is that of the Muskeget Beach mouse (*Microtus breweri*) a derivative of the common brown meadow mouse of the New England mainland. On this island of white sand off the Massachusetts coast, a pale variety has developed which is very distinct from that of the neighboring shores. Not only is it a paler race, but albinism also has begun to appear, so that occasional individuals have a white fleck between the ears, showing the drawing apart of the ear patches. Of a series of 62 specimens in the collections of the Museum of Comparative Zoology and the Boston Society of Natural History, no less than 13 had such white flecks, and one had in addition a white spot just in advance of the shoulders, marking the line of separation between neck and shoulder patches. In our studies on the heredity of coat colors in mice, Professor Castle and I discovered (Allen, 1904; see also Little, 1914) that the pied condition is recessive in the Mendelian sense towards the self colored, so that partial albinos bred to wholly pigmented mice produce in the second generation, if interbred, 25 per cent. of spotted young. The figures

given above (13 in 62) are near this in case of the Muskeget mouse, but the matings are of course more promiscuous. The case is interesting in connection with the studies of Ramaley (1912) and Pearl (1914), tending to show that in a mixed population the recessives may increase so as to exceed the dominants. Although the spotted mice do not, in case of this species, exceed the unspotted individuals, they nevertheless are of far more frequent occurrence than they are in the mainland representatives of the species. This accords with the fact that island-living mammals are very commonly albinistic, and the cause is doubtless that the population is much more inbred, so that the recessive condition of partial albinism is more likely to be propagated than if successive generations have a wider range over which to spread. It seems probable that heredity will tend to increase the proportion of spotted mice of Muskeget, and that if this condition is disadvantageous, a large part of the spotted individuals will be killed off, yet in the course of time they may become adjusted to this condition and will survive in increasing proportion till the white mark becomes characteristic of all the animals. Cory (1912) records the capture of seven muskrats at Hayfield, Iowa, all of which were uniformly marked, having a white ring around the neck and the entire underparts, feet, and end of tail white. I can think of three causes influencing the status of such white markings. These markings may be inherited in a purely automatic way as unit characters; but if thus inherited they may be (1) increased through selection, natural or sexual; or (2) eliminated by the same agent; or (3) they may be, at first, of no influence at all in the economy of the animal and persist or not, according as they are heritable.

I have mentioned that island mammals tend to be more albinistic than their mainland representatives. Other cases may be mentioned, as the common squirrel (*Sciurus vulgaris leucurus*) of Great Britain, which differs notably from that of the continent in having frequently a

white or whitish tip to the tail, often for one half its length. A similar white tip is occasionally seen in our red squirrel (*S. hudsonius*) as an albinistic mark, and is due, of course, to the terminal restriction of the rump patches. The deer of Whitby Island, Puget Sound, are said to be much marked with white, and sundry marsupials of Papua as well as the monotreme *Zaglossus* are subject to white markings. In the cuscus (*Pseudochirus*) the pigment is sometimes restricted to small patches and round spots scattered on the back, those in the region of the shoulder of a different color from those of the side and rump patches. Another instance is that of the white-footed mouse of Monomoy Island, Massachusetts, the mid-ventral parts of which are pure white to the roots of the hairs, an albinistic condition to be clearly distinguished from that in which the belly appears white, but only because of the white *tips* to the hairs whose bases are dark-pigmented.

The restriction of the rump patches so as to produce a white tail-tip is common among mammals. It is found in occasional specimens of many species as the shrew mole (*Blarina*), Brewer's mole (*Parascalops*), the meadow jumping mouse (*Zapus*), the white-footed mouse (*Peromyscus*), and squirrels (*Sciurus*). In some it has become developed as a permanent and characteristic mark, as in the woodland jumping mouse (*Napæozapus*), the red fox (*Vulpes*), such genera as *Hydromys, Tylomys,* the Virginia opossum (*Didelphys virginiana*), the tree kangaroos (*Dendrolagus*). In many others a pure white belly is developed through ventral restriction of the shoulder and side patches.

Among ungulates the break between the ear patches has been developed to form a broad white blaze from forehead to nose in case of the blesbok (*Damaliscus albifrons*) of South Africa and in related species in East Africa. The chevron-mark on the forehead of certain antelopes is possibly a specialized development of the same thing.

White buttock patches are present in several unrelated ungulates—as the pronghorn (*Antilocapra*), the wapiti (*Cervus canadensis*), and the Rocky Mountain sheep (*Ovis canadensis*). Probably these are the result of restriction or total inactivity of the pigment patches covering the rump.

FIG. 42*a*. DIAGRAM SHOWING THE PIGMENTED PATCHES OF A PARTIALLY ALBINO DEER.

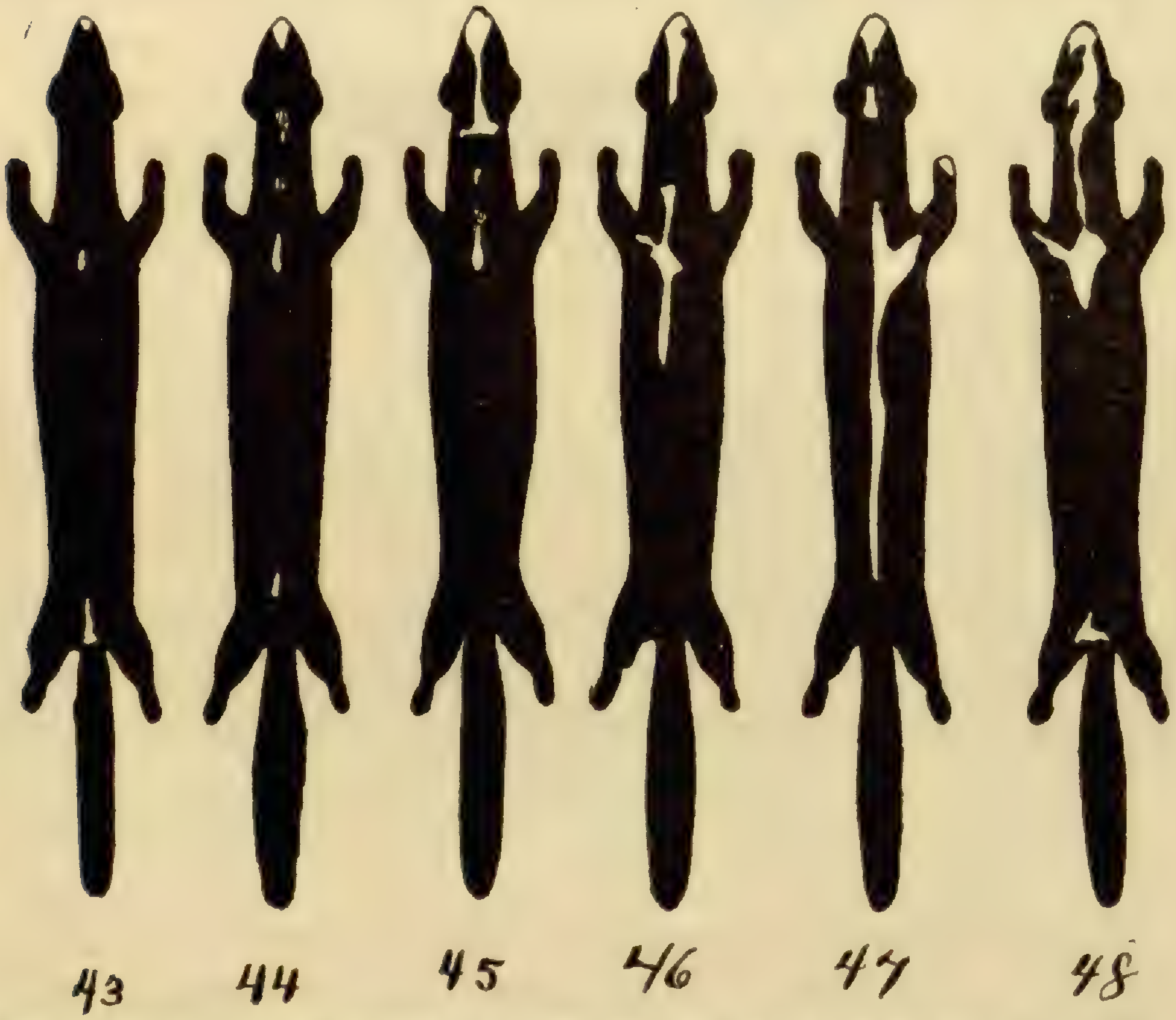
Among the deer family white is generally confined to the under surfaces and the primary white breaks have not been developed to form patterns. Albinistic deer are fairly common, however, and in Fig. 42*a* I have made a tracing from a photograph showing the side of a partially albino doe in which areal restriction of pigment has taken place in such wise that the primary patches are all indicated, and separated from those of the opposite half of the body by a median dorsal white line. The ear and the neck patches are joined, but a few small islands of pigment are left here and there, much as in cows.

In the young of many deer and in the adult of such species as the axis deer, a spotted pattern is developed.

There is an obvious tendency for the spots to become arranged in longitudinal rows, and intermediate stages may be found in which they coalesce to form broken lines. There is little doubt that the complete white stripes occurring in part of this pattern were formed originally through the coalescence of rows of white spots. In the tapir a somewhat similar spotted pattern is found in the young, while the adult Malayan tapir has lost the shoulder and side patches, producing thus a white-bodied animal, pigmented to the back of the foreleg and on the buttocks and hind legs. Among the ground squirrels (*Citellus*) a beautiful series can be picked out showing the transition from a uniform grizzled mixture of ticked hairs to indistinct spotting, then rows of white spots, and finally broken and complete longitudinal stripes. The production of these stripes I believe to be due, not to the development of breaks between the primary pigment patches, but to the action of a factor which is the negative of the so-called "English" marking in rabbits, so that instead of the *development of scattered small pigments spots* there are formed, instead, spots without pigment. That it is possible to evolve a striped pattern from spots through selection, I have no doubt, and indeed, it is generally believed. On the other hand, it is quite possible that the converse may happen, and spots result through the breaking up of stripes. According to the experiments of Professor Castle and Dr. MacCurdy, however, it seems to be a difficult matter to fix a given marking by rigid selection, yet it must be admitted that a few years' work even of careful breeding is nothing in comparison with the age-long selection that may have been at work on the species. That it is a difficult matter to produce a given pattern is further evidenced by the fact that in many species in which white markings regularly occur as part of the pattern, these are subject to great individual variation in their extent, showing that they are even yet not wholly definite.

It was formerly urged against evolutionary doctrine

that we do not now see its processes in action, that species are stable and subject to very little variation. This view, however, was found to rest on faulty observation, for, though some species are fairly stable, others are very plastic and exhibit before our eyes various steps in development. So in case of the development of a particular pied pattern, it is possible to see in certain species the actual course of its formation. Among mammals, the Mustelidæ or weasel family show several instances in



FIGS. 43–48. DIAGRAMS SHOWING RESTRICTION OF PIGMENTATION ON THE VENTRAL SURFACE OF MINKS (*Mustela vison*).

point. The common mink (*Mustela vison*) of northeastern North America is now in process of developing a pure white under side, such as is present in the New York weasel (*M. noveboracensis*) or the smaller Bonaparte's weasel (*M. cicognani*). The diagrams shown in Figs. 43–48 are from the fine series of mink in the collection of the Museum of Comparative Zoology and depict the

under side of the specimens. In the large coastal race of mink found from southern Maine to the Carolinas (*M. v. lutreocephalus*), the entire pelage is usually brown, except for the chin which is white. Occasional white marks are present in some specimens along the mid-ventral line of the throat and chest, and between the hind legs. In the smaller typical *M. vison* of northern New England northward the white marking is apt to be more extensive, and in no two individuals exactly alike. The diagrams show the ventral markings of a few specimens from New England and Nova Scotia. In Fig. 43 the amount of white is very small. The chin spot, which represents the beginning of a break between the two ear patches at their antero-ventral extremity, is always present and has become now a fixed mark of the species, though variable in extent. A slight break in the center of the chest shows where the two shoulder patches have failed to meet, and a white spot at the anal region indicates a like restriction of the rump patches. Similar spots appear mid-ventrally in Fig. 44, with the addition of a few white hairs, medially at the upper throat, where the ear and neck patches join, and a few more on the lower throat at the line of union of the neck patches of opposite sides. In Figs. 45 and 46 no break is present on the abdomen, but in the former figure, a large transverse break has appeared on the upper throat where the ear patches fail to unite with the neck patches and with each other, and a median line runs forward to join the white of the chin, showing the greater restriction of the ear patches ventrally. An imperfect separation of these patches along the center of the throat has taken place in Fig. 47, and a more considerable break occurs in the same place in Fig. 46. In the Pacific Coast mink (*Mustela vison energumenos*) a well-developed white patch on the chest is rather characteristic, somewhat larger than in Fig. 45. This is due to the ventral restriction of the shoulder patches which fail to meet below. In Fig. 46 this white area is seen with a tongue extending upon the center of the lower throat, and on to

one fore leg, as well as in the mid line of the thorax, marking nearly the anteroposterior limits of the shoulder patch. The neck patches are not separated in this figure but have become so in Fig. 48, so that a continuous line of white runs from chin to chest. In Fig. 47 the shoulder and the side patches have both failed to join ventrally, and thus a broad white line is formed down the center of the belly from the conjoined neck patches to the rump patches. If all these breaks were to be present in a single animal, there would be a narrowed white area along the entire ventral side of the body from chin to anus, extending on to the lower side of the fore legs. Practically this condition exists in another species of the same genus, Streator's weasel (*Mustela streatori*) of the Pacific Coast, in which the throat, chest and belly are white but the width and boundaries of the white area are very variable in different individuals. It is therefore in a stage beyond that which the minks have reached, yet it has not attained the stage in which the white area is of definite and rather constant bounds, as in certain other weasels, for example *Mustela noveboracensis,* in which the white, of the belly extends nearly or quite to the lateral border of the body, but in different individuals varies slightly, and *M. cicognanii,* in which the white area of the belly constantly extends to the lateral boundary of the venter from throat to anus. This is the condition toward which the mink is tending.

Another interesting case in which a pattern mark appears to be evolving through the fixation of a primary break between pigment patches is that of the so-called tayra of South America (*Tayra barbara*) a large Mustelid. The Central American race (*biologiæ*) of this animal is wholly black, but the typical subspecies of Brazil and northern South America is subject to a varying amount of reduction in pigmentation. Curiously, this takes place at the posterior end of the neck patches or at the anterior part of the shoulder patches. Three of five specimens in the Museum of Comparative Zoology are marked in this

way. All have a triangular patch of white at the base of the throat ventrally, as a break between neck and shoulder patches and a partial separation of the neck patches from each other. Each has a *dorsal* mark of white; in the first a narrow linear break between the shoulders; in the second a broader transverse mark, and in the third a square patch of white occupying nearly the width of body between the shoulders to the base of the neck. The white throat marking increases in extent from first to third, just as does the dorsal marking. Probably in time this white mark, now of irregular size and appearance individually, will become a permanent part of the pattern. In this animal the entire head and neck are a grizzled gray as far back as the posterior limit of the neck patches, and the rest of the body is black. This, then, shows that the pigment patches of head and neck are differentiated in color as well, from the patches of the rest of the body. The occurrence of white markings in the back is relatively uncommon in mammals, though white on the under surfaces is common, and, as shown by Mr. Abbott H. Thayer, may be of real service to the animal as a factor in concealment.

In the development of white pattern-marks, the evidence seems to show that these come in at first as small and fluctuating spots, which may be of little effect in the economy of the animal. Their further development might lead to the extinction of the species if they render it too conspicuous to enemies, unless the species at the same time makes use of them or accommodates itself to their revealing effect. Often, no doubt, they may not be a source of danger at all. A case in point may be that of *Sciurus finlaysoni,* a Malayan squirrel, most of the individuals of which are largely marked with white, and of which specimens may be found side by side, varying from an almost entirely pigmented condition to one of completely white coat and black eyes. White squirrels are occasional in other species, as albinos, but these rarely survive more than a generation in the cases I have known, whereas

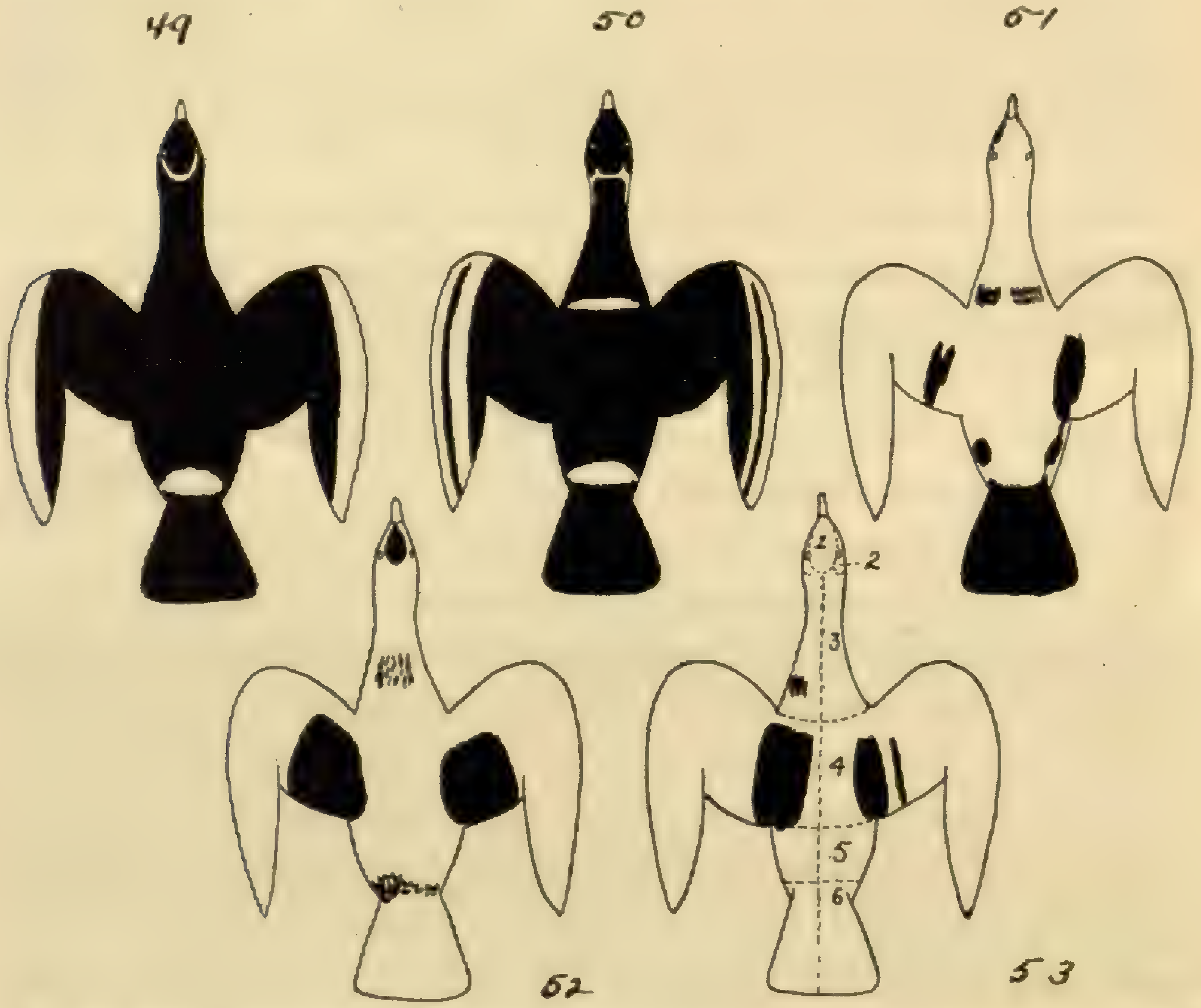
Finlayson's squirrel seems to have accustomed itself by gradual stages to the white condition, so that it is probably not at a great disadvantage by reason of its whiteness.

Pigment Patches in Birds

In birds the same primary pigment patches seem to be present as in mammals, and they are homologous in the two groups. In defining the extent of the pigment patches, however, allowance must be made for the fact that the long feathers may cover a part of the body remote from their origin. The distribution of the feathers or the pterylosis of the species in hand must also be remembered. In order to arrive at the true interpretation of the patches, it is necessary to consider the pigment as projected back from the vanes of the feathers to the part of the body at their bases. By so doing, it becomes evident that a feather variegated with pigmented and unpigmented (or white) areas indicates none the less that the feather arises from a place of pigment formation. It is only a wholly white feather or patch of feathers that can be considered albinistic in the sense here intended. The factor determining the intermittent formation of pigment in the individual feather is probably a wholly different one from that determining the presence or absence of pigment formation at certain places on the body, though not necessarily different except in its intermittent action.

In the domestic pigeon of our streets and buildings, we have a species that in its wild state is normally fully pigmented except for a white rump patch. Under semi-domestication it has developed partial albinism to a large degree, so that it is possible to obtain a complete series representing on the one extreme a totally pigmented bird without a trace even of the white rump patch, and on the other extreme a bird of pure white plumage. A few of the intermediate stages in areal reduction of pigmentation are shown in Figs. 49 to 53, selected from birds raised for the market and, so far as known, not

bred for pattern. The first steps in reduction are shown in Fig. 49. Here there is seen first a crescentic band of white feathers passing from eye to eye around the occiput. This is a primary break marking off the crown patch posteriorly. This patch in birds, in contrast to its development in mammals, is the main patch of the head,



FIGS. 49–53. DIAGRAMS SHOWING PIGMENTATION IN THE DOMESTIC PIGEON.

covering the area from the base of the bill to the eyes and occiput. In Fig. 50 its posterior limit is similarly defined by a primary break separating it from the neck patches, and although it does not extend forward quite to the eye in this specimen, it shows a beginning of separation from the more lateral ear patches by virtue of the indentations on each side posteriorly. In Fig. 52, the crown patch is shown slightly reduced in extent and wholly separate from the ear patches, which have become inactive altogether. In Fig. 53 it has dropped out with the latter. It is evident then that by greater or lesser

reduction of the crown patch alone it is possible to produce a pigeon with a mere white spot at the back of the head, one with a white stripe from the base of the beak through the eyes to the back of the head (or some part of such a stripe) to a pigeon in which by the total reduction of the patch, the entire top of the head is white. Such specimens can be found in most any miscellaneous flock. There is a tendency often for the patch to be irregularly broken, sometimes divided almost into two parts, a result of the pterylosis to some extent.

The ear patches in pigeons, and probably in all birds, are rather insignificant, and the smallest of all the primary pigment areas. They include the feathers from the posterior angle of the lower mandible to the angle of mouth and thence back, including the ear coverts. I do not feel sure that the patches of opposite sides may not join on the chin, but the present evidence tends to show that the chin is pigmented by a forward extension of the neck patch, which, under reduction, often leaves a small island of pigment between the mandibular rami. In Fig. 50 the neck patches are seen to have broken away anteriorly from the crown and ear patches and the separation of the latter from the crown is indicated by deep reentrants along the line of the separation. In Fig. 51 a remnant of the ear patch of the left side alone remains in dorsal view, consisting of a small tuft of pigmented feathers at the fore end of the aural area and a single pigmented feather just behind it. In this specimen there are a few pigmented feathers on the chin as well, which I take to be an isolated bit of the neck patches.

The neck patches are bilateral in origin, and pigment the entire throat and neck back to a point corresponding to the base of the neck vertebræ. They meet the crown patch and separate the ear patches at the occiput. In the domestic pigeon the neck patches correspond very closely to the area of differentiated feathers that give the metallic reflections. In the reduction of this area it is common for the anterior part of the throat to be white, and then a

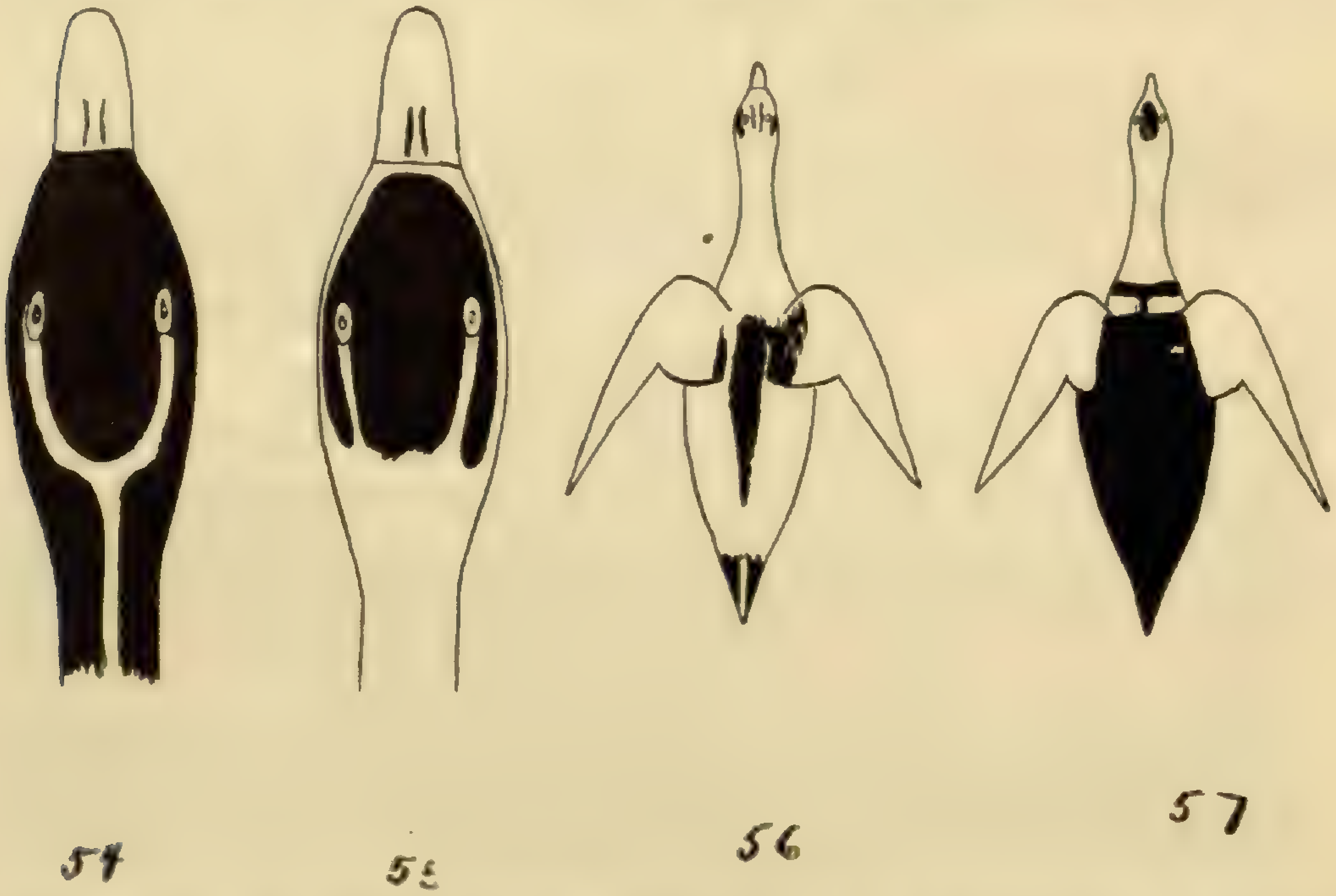
break occurs between the neck patches and those of the head as in Fig. 50. Posteriorly the neck patch under reduction may become separated by a white ring at the base of the neck, from the shoulder patches as in Fig. 50. The ultimate centers of these patches seem to be in the pigeon well back on the base of the neck. These are shown, of small extent, in Fig. 51, as two small areas of pigmented feathers, one on each side of the base of the neck. In Fig. 53, further reduction has taken place, so that the patch of the left side only remains as a small center. In Fig. 52 there is a large median dorsal patch, which, as in mammals, may represent the two centers of opposite sides which even under much reduction have not in this individual become divided medially.

A very common manifestation of pigment reduction in pigeons is to have the primaries or some of them white, as in Figs. 49 or 50. This indicates a failure of pigment to develop at the extremities of the shoulder patches, just as in mammals white forefeet mark a slight reduction of the same areas. It is a fact of much interest that in the guinea fowl (*Numida*), which has been under domestication but a short time comparatively, a distinct breed has arisen in which this same reduction of pigment is present, resulting in a speckled bird with pure white primaries and often a pure white area on the breast. In the pigeon, further reduction cuts off a narrow ring of pigment encircling the breast, or, it may be, broken in the mid-ventral line. This ring represents the reduced shoulder patches, and is to be seen in many wild species as a permanent part of the pattern. The white collar at the base of the neck in Fig. 50 marks the separation between the neck and the shoulder patches at the anterior border of the latter. In other specimens the patches are separated medially by a white area down the back. The ultimate centers of these patches seem to be near the elbow or on the upper arm at the base of the tertiaries, as seen in Figs. 52 and 53.

The side patches are rather small and seem to center, as in Fig. 51, near the groin on either side. They pigment the belly back of the breast area included by the shoulder patches, and extend on to the hind legs as well. In a specimen before me, the shoulder patches pigment the bases of the wings and the entire breast corresponding roughly to the length of the sternum, and tend to be separated by encroaching white feathers midventrally. The side patches are much more reduced, and are confined to a small area at the top of each thigh. The remainder of the patches has become inactive, so that a completely white belly and back result. A very common occurrence is the white rump patch due to the restriction of the side patches, so that a break occurs between them and the tail patches. The rump patches in birds are situated far back, as in mammals, and pigment the tail coverts and the rectrices as in Figs. 49–51. The bilaterality of the two patches is often indicated in pigeons by the occurrence of a few pure white rectrices in the center of the tail. Other birds show pure white feathers at either side of the tail, with a tendency to bilateral symmetry, a most important fact, since it indicates restriction at the outer extremes of these centers. In the restriction of pigment formation, the rectrices are the first to become white, as one would expect, since they are situated at the extremity of the body and farthest from the center of the patch. In Fig. 52 these centers are seen to be at the base of the tail above, and include the upper tail coverts. They are still joined medially, but that of the left side is more extensive than the patch on the right side. The approximate boundaries of the several pigment patches are indicated in Fig. 53 by dotted lines; 1 is the crown patch, 2 the ear patch, 3 the neck patch, 4 the shoulder patch, 5 the side, and 6 the rump patch, as they appear in a dorsal view. Ventrally the neck patch runs forward to the symphysis of the mandibles.

In a flock of domesticated mallard ducks which I studied, the same patches were found indicated, and

some of the details of these are shown in Figs. 54–56. In the male wild mallard there is no white in the pattern of the head and neck except a white ring at the base of the neck. In one of the domesticated breed, shown in Fig. 54, the crown patch was very beautifully marked off, as in the pigeon (Fig. 49), by a white band from eye to eye passing about the occiput. This duck was further interesting in showing the median division of the two neck patches, as a narrow white line running down the



FIGS. 54–57. DIAGRAMS SHOWING PIGMENTATION IN DOMESTICATED MALLARD DUCKS AND IN THE (WILD) LABRADOR DUCK (57).

back of the neck medially, from the occipital stripe. Another duck shown in Fig. 55 had lost the neck patches entirely, but showed the same occipital stripe bounding the crown patch posteriorly, and the ear patches dorsally. The ear patches still adjoin the crown patch anteriorly. In Fig. 56 is represented another of these ducks in which both ear patches are distinct and separate on either side of the head. The crown patch appears as two narrow lines of pigmented feathers which are not quite in contact posteriorly. I have not obtained a satisfactory explanation for the apparent tendency of this patch to

divide medially. Probably for some reason the formation of the pigment is more intense at the sides of the crown than in the center where the nerve and blood supply is less. In the pterylosis of this area the development of feathers is seen to be greater at the sides also.

The neck patches and the side patches are absent entirely, but the shoulder patches are both present, in Fig. 56, that of the right side covering the scapulars and middle of the upper back, that of the left side including a few only of the scapulars.

The tail patches are both present, and separate from each other, as shown by the median white rectrices.

In this same flock of mallards was a female which had a white ring at the base of the neck in the same situation as the white ring which in the male is a part of the permanent pattern. It was not quite complete dorsally, however, in this female, and was somewhat broader than regularly in the male. Nevertheless, it is apparent that this white collar in the male is merely a primary break between neck and shoulder patches that has become developed as a part of the normal pattern.

Stone (1912, p. 318) in his paper on the phylogenetic value of color characters in birds, hints at the existence of these patches. He says, in part:

> In matters of pattern there seems to be a deeper problem involved, *i. e.*, the determination of the cause governing the appearance of a differently colored patch on corresponding parts of the plumage of birds belonging to wholly different groups . . . or the presence of a mystacial stripe, a superciliary stripe, a light rump patch. . . . In fact if a bird exhibits a bright or contrasting patch of color, it is, in the vast majority of cases, found on one of several definite portions of the plumage, as the crown, the throat, the bend of the wing, the rump, etc.

These contrasting areas are due to the development of one or more of the primary patches, or of breaks between them, or again paler areas, as at the bend of the wing or on the rump, indicate often a lessening of pigment intensity at a distance from the respective primary centers.

(*To be concluded.*)

NOTES ON THE MEADOW JUMPING MOUSE (ZAPUS HUDSONIUS) ESPECIALLY REGARDING HIBERNATION

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DEDHAM, MASS.

THE jumping mouse is the only one of the wild mice of this region (Massachusetts) which exhibits the habit of regular hibernation. Regarding this habit there are a number of references in the literature on the subject. Barton[1] was one of the first to refer to the fact that this mouse became dormant in winter. He says, in describing the actions of one he had in captivity:

> On or about the 22d of November it passed into the torpid state. It is curious to observe that at the time it became torpid the weather was unusually mild for the season of the year, and moreover the animal was kept in a warm room, in which there was a large fire the greater part of the day and night . . . It was frequently most active while the weather was extremely cold in December.

This was in Philadelphia, Pa.

Audubon and Bachman[2] regret that they live in a region where the species does not exist and can not speak from personal observation on the subject.

Godman,[3] Thompson[4] and Kennicott[5] speak of its habit of hibernation.

Tenney[6] gives an account of a specimen of this species taken alive on January 18, 1872, near Vincennes, Ind. It was dormant, coiled up tightly, "the nose being placed upon the belly, and the long tail coiled around the ball-like

[1] "Some Account of an American Species of Dipus or Jerboa," by Benjamin Smith Barton, M.D., *Translations of the Am. Philosophical Society,* Vol. IV, No. XII, 1799.

[2] Viviparous Quadrupeds of No. America," Vol. II, 1851, p. 255.

[3] Godman, "Am. Nat. Hist.," Vol. I, 1842.

[4] Rev. Zadoc Thompson, "Nat. and Civil Hist. of Vermont," 1842.

[5] Kennicott, Patent Office Report for 1857.

[6] Tenney, "Hibernation of the Jumping Mouse," AM. NATURALIST, June, 1872, Vol. VI, No. 6, pp. 330–332.

form which the animal had assumed." It was taken from a nest about two feet below the surface, made of bits of grass. The mouse showed no signs of life at first, but on being held in his hand, soon became feebly active, and on being placed in a warm room, came out of its dormant condition entirely. It again became dormant that night, but was aroused twice again by the application of heat, within the next few weeks, in spite of very cold weather.

Merriam[7] tells of taking an active male at Easthampton, Mass., on February 11, 1872, and states that during the mild winter of 1881–82, in Lewis County, Northern New York, he saw jumping mice active several times.

Seton[8] speaks of finding a *Zapus Hudsonius* on September 27, 1888, at Carberry, Manitoba, in a nest of leaves under the roots of a stump, nearly torpid. He says:

> In the country near Carberry, I never saw it active after September first.

Stone and Cram[9] believe that this mouse passes six months or more of every year hibernating underground. They speak of seeing a family of them turned up by a plough in May and exhibiting not the slightest symptom of life, on being handled or breathed upon.

Burroughs[10] tells of a female jumping mouse in captivity that began hibernating early in November and continued until May, with several intervals of activity, especially after warm weather came on.

Preble[11] says:

> Hibernation varies with the locality, but usually begins about the time of the first heavy frosts and lasts until Spring. The fall pelage is usually assumed and the animals become exceedingly fat before entering winter quarters. Although they often lay up stores of food in nests or burrows during summer, it is not known that they use this food during winter. The animals are generally found singly (sometimes in pairs) in nests at a depth varying from a few inches to two or three feet below the surface. Hibernation sometimes takes place above ground.

[7] C. H. Merrian, M.D., "Mammals of the Adirondack Region," 1884.

[8] E. T. Seton, "Life-histories of Northern Animals," Vol. I.

[9] Stone and Cram, "American Animals," p. 103–104.

[10] John Burroughs, "Squirrels and Other Fur Bearers," pp. 121–124.

[11] E. A. Preble, "Revision of the Jumping Mice of the Genus *Zapus*," U. S. Dept. Agr. N. A. Fauna Series, No. 15, 1899.

On June 25, 1912, a female *Zapus Hudsonius* was taken alive, by the writer, on the edge of a small pond in eastern Massachusetts. It was placed in a small wire cage, and after a few frenzied efforts to escape, became quite tame. On July 5 it gave birth to five young, blind and hairless; but when the family was transferred to a larger cage, the mouse deserted the young and they soon died. One disappeared mysteriously, and may have been eaten by the mother. The young measured at birth: total length 33 mm.; tail 9 mm.; hind foot 4 mm.

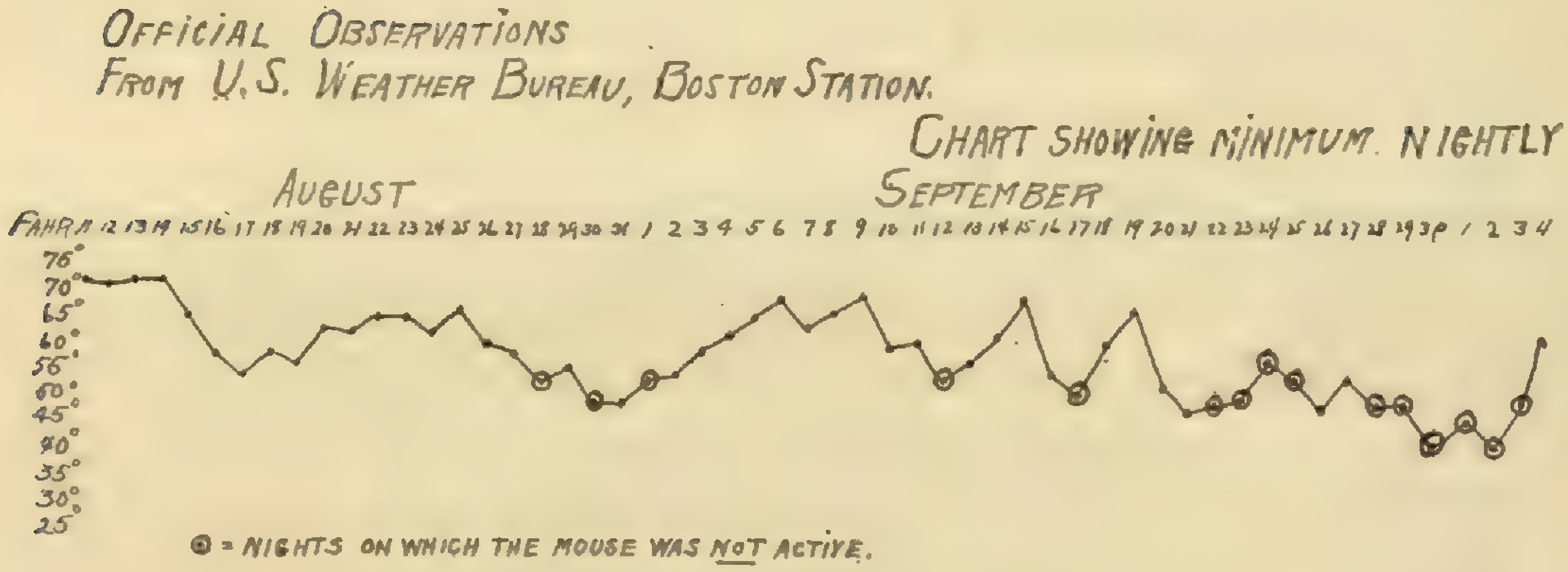
Throughout the summer the mouse ate chiefly rolled oats and shredded wheat, and was also very fond of strawberries and blueberries. It refused most of the common fruits and vegetables.

It was almost wholly nocturnal in its activity, although when disturbed during the day it would immediately begin to eat and remain active for half an hour or more. Toward the latter part of the summer, it seemed to grow quite fat. Rhoads[12] says in this connection:

> When going into winter quarters they are exceedingly fat, as I can testify from experience in removing this tenacious yellow blanket from the skins of them. This fat is their fuel. By spring it is nearly gone.

During the latter part of August there were several very cool nights (49° F. minimum) and on the night of August 28 it did not come out. This fact was apparent from the clean drinking dish, which was placed in such a position that the mouse could not approach without scattering saw-dust in it. The absence was repeated on August 30, and September 1. Throughout September its actions were irregular. Every night until the 21st, with the exception of the 12th and 17th, it was active, but on the 22d disappeared for four nights. It was then active for two more nights (26 and 27) and following that, inactive for six (September 28 to October 3). From October 4 to 28 it was out every night, although not as vigorous as formerly, neither did it eat as much. When approached it seemed to pay no heed, as if in a sort of stupor.

[12] S. N. Rhoads, "The Mammals of Pennsylvania and New Jersey."



There was no evidence of any attempt at storing away a supply of food, although there was ample opportunity. This habit of storing food is mentioned by Hornaday[13] who says:

In the autumn it stores in the ground quantities of food for winter use, but despite this fact, under certain conditions, it becomes so thoroughly dormant in winter that it seems to be quite lifeless.

According to Seton,[8]

It is quite ready to respond at any time to any spell of unusually fine, unseasonable weather, even in the depths of winter, and it is probably for these arousing times, as much as for the spring time famine, that it lays up its abundant stores of food.

Preble[11] also mentions this habit, but Shufeldt[14] denies it. He says, in speaking of the deer mouse (*Peromyscus Leucopus*):

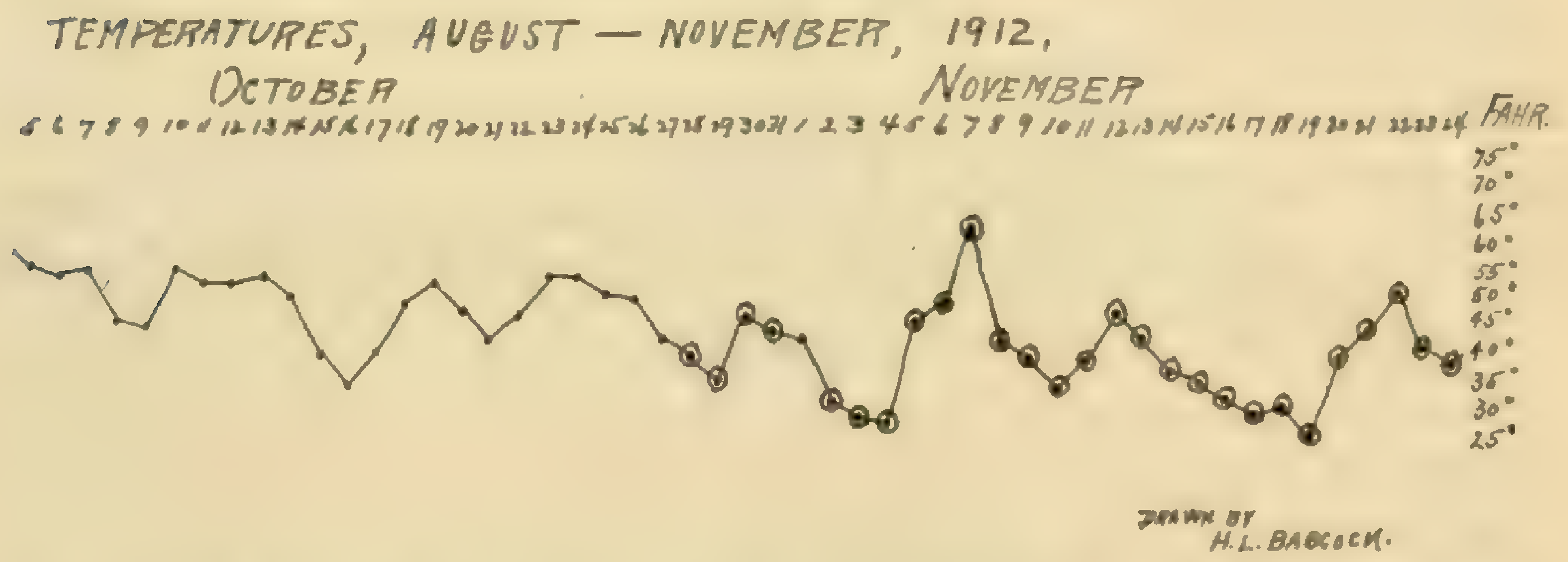
Is it to meet the requirements of his condition that this mouse lays up a goodly stock of food during the autumn? Something the *Zapus* does not do.

Following the period of activity through October, the mouse was inactive on the four nights of October 28, 29, 30 and 31, and reappeared for the last time on the night of November 1, after which it retired for the winter. The cage was placed by an open window of an empty box stall in a stable where the temperature was practically that of out doors. The mouse built its nest in the side of a large sod placed in one corner of the cage.

In spite of a very mild winter, the lowest official tem-

[13] Hornaday, "The American Natural History."

[14] R. W. Shufeldt, M.D., "Chapters on the Natural History of the United States."



perature for this section being only 3° F. (February 10, 1913,) the mouse did not survive the cold weather, and was found dead, when the cage was opened on June 17, 1913.

The nest was found to be located in the extreme end of the sod, only 1½ inches from the top and about 1 inch from the edge. It was roughly oval in shape, being hollowed out of the loam and lined with a few blades of grass. It measured roughly 1¾ inches by 1½ inches and was just large enough to contain the mouse when curled up into a ball. The opening was on the side. Death was probably caused from exposure to continued cold owing to the unprotected location of the nest.

The poor judgment shown in not building the nest securely in the middle of the large sod, and other similar instances of poor management, have led the writer to believe that the intelligence (if that term may be used) of the *Zapus Hudsonius* is of comparatively low grade, much lower, for instance, than that of the deer mouse (*Peromyscus Leucopus*).

The accompanying chart, which is a record of minimal nightly temperatures, according to the official observations of the U. S. Weather Bureau for this section (Boston), shows the activity of the mouse in relation to the temperature during August, September, October and November, and brings out some rather interesting facts. For example, on October 15, 16 and 17, with the minimum nightly temperature 42°, 36° and 42°, respectively, the mouse was active, while on September 22, 23, 24 and 25,

with the minimum nightly temperature of 48°, 49°, 56° and 53° F., respectively, a much warmer series of nights, it remained inactive, And again, after November 1, during a warm spell in which the minimum nightly temperature for November 7 was 64° F., the mouse did not appear.

A study of this chart suggests the question as to how much the temperature has to do with this habit of hibernation.

It is a somewhat general belief that temperature regulates the degree of torpidity.

Barton[1] maintains that

the torpid state of animals is altogether an accidental circumstance and by no means constitutes a specific character. The same species becomes torpid in one country and not in another. Nay, different individuals of the same species become torpid or continue awake in the same neighborhood or even on the same farm.

Seton[8] believes that

while torpor is more or less controlled by temperature, the habit of torpidity, like the changing pelage of the white-hare, is so deeply ingrained constitutionally that there is a strong tendency to torpify at a given time without regard to the original cause.

It is evident from this chart that torpidity develops gradually, at first for only one night at a time. Whether this process is explained by a cerebral anemia, a slow toxemia of the brain centers or some other of the theories regarding sleep, it seems to require about two months in which to become sufficiently developed to control completely voluntary body functions. During that interval the animal occasionally awakens, probably from hunger and habit as much as from any effect in change of temperature.

After torpidity is thoroughly established, changes of temperature may be important external factors, as has been demonstrated on numerous occasions in producing a temporary activity by the application of heat. It is safe to say, however, that the temperature is not the only element which influences the length of the period of hibernation.

SHORTER ARTICLES AND DISCUSSION

STUDIES ON INBREEDING—IV

On a General Formula for the Constitution of the nth Generation of a Mendelian Population in which all Matings are of Brother × Sister [1]

I. In a former paper in this series[2] the constitution of a Mendelian population in which all mating was of the brother × sister type was worked out empirically. The results there presented may be put in the form of a general formula, by means of which the constitution of any generation may be written down from a knowledge of the preceding generation; that is from a knowledge of the $n-1$th generation the nth generation may be at once written down.

II. This general formula may be developed as follows. A single character pair will be considered, A denoting the dominant character and a the recessive. Equal fertility for all matings is assumed, the number of individuals per family being taken as $2s$, of which s are males and s are females. One family will then make s matings and produce s families in the next generation. Each mating is, by hypothesis, of a brother with his sister.

Starting as before with a pair from a population in which all individuals are of constitution Aa there will be in the next generation one family of the $AA + Aa + aA + aa$ type. In all succeeding generations there will be six types of families, viz.:

(1) AA families.
(2) $AA + Aa$ families.
(3) Aa families.
(4) $Aa + 2Aa + aa$ families.
(5) $Aa + aa$ families.
(6) aa families.

[1] Papers from the Biological Laboratory of the Maine Agricultural Experiment Station, No. 66.

It seems desirable to publish as a general series of "Studies on Inbreeding" the results of certain investigations now in progress in this laboratory. The three papers which have already appeared in this series, without the general title, are: I. "A Contribution towards an Analysis of the Problem of Inbreeding," Amer. Nat., Vol. XLVII, pp. 577–615, 1913. II. "Tables for Calculating Coefficients of Inbreeding," Ann. Rept. Me. Agr. Expt. Sta. for 1913, pp. 191–202. III. "On the Results of Inbreeding a Mendelian Population: A Correction and Extension of Previous Conclusions," Amer. Nat., Vol. XLVIII, pp. 57–62, 1914.

[2] Amer. Nat., Vol. XVLIII, pp. 57–62, 1914.

The proportionate number of each of these types of families will change in successive generations according to the following system.

Let o_{n-1} denote the number of AA families in the $n-1$th generation, and

p_{n-1} denote the number of $AA+Aa$ families in the $n-1$th generation, and

q_{n-1} denote the number of Aa families in the $n-1$th generation, and

r_{n-1} denote the number of AA and $2Aa$ and aa families in the $n-1$th generation, and

u_{n-1} denote the number of $Aa+aa$ families, and

v_{n-1} denote the number of aa families.

It will be possible to write down u and v in any case without calculation because of the symmetrical relations of a Mendelian population, since always under normal conditions such as are assumed in the general treatment, we have

$$u_{n-1}=p_{n-1},$$
$$v_{n-1}=o_{n-1},$$
$$u_n=p_n,$$
$$v_n=o_n.$$

It is necessary, therefore, to consider only the coefficients for the first four types of family. In the nth generation the constitution of the population in respect of *families* (not individuals) will be as follows:

Families in nth generation

$$\begin{aligned}&=s(o_{n-1}+1/4p_{n-1}+1/16r_{n-1})AA \text{ families}\\&+s(1/2p_{n-1}+1/4r_{n-1})AA+Aa \text{ families}\\&+s(1/8r_{n-1})Aa \text{ families}\\&+s(1/2p_{n-1}+q_{n-1}+1/4r_{n-1})AA\\&\qquad+2Aa+aa \text{ families}\\&+s(u_n)Aa+aa \text{ families}\\&+s(v_n)aa \text{ families.}\end{aligned}$$

Or, taking coefficients alone we have

$$\left.\begin{aligned}o_n&=o_{n-1}+1/4p_{n-1}+1/16r_{n-1},\\p_n&=1/2p_{n-1}+1/4r_{n-1},\\q_n&=1/8r_{n-1},\\r_n&=1/2p_{n-1}+q_{n-1}+1/4r_{n-1},\\u_n&=1/2u_{n-1}+1/4r_{n-1}=p_n,\\v_n&=v_{n-1}+1/4u_{n-1}+1/16r_{n-1}=o_n.\end{aligned}\right\}\quad\text{(i)}$$

III. Let us see how this formula works out in a concrete case. Assume the same conditions of fertility as in the former paper, that is, put $2s = 32$, or $s = 16$. Start with a single $AA + 2Aa + aa$ family.

Then

$$o_{n-1} = 0,$$
$$p_{n-1} = 0,$$
$$q_{n-1} = 0,$$
$$r_{n-1} = 1.$$

Then in the next generation we shall have

$16\{0 + 1/4(0) + 1/16(1)\} = 1$AA family
$+ 16\{1/2(0) + 1/4(1)\} = 4(AA + Aa)$ families
$+ 16\{1/8(1)\} = 2Aa$ families
$+ 16\{1/2(0) + 0 + 1/4(1)\} = 4(AA + 2Aa + aa)$ families
$+ 4(Aa + aa)$ families
$+ 1aa$ family.

This is the fact.

In the next generation we shall have

$16\{1 + 1 + 1/16(4)\} = 36AA$ families
$+ 16\{1/2(4) + 1/4(4)\} = 48(AA + Aa)$ families
$+ 16\{1/8(4)\} = 8Aa$ families
$+ 16\{1/2(4) + 2 + 1/4(4)\} = 80(AA + 2Aa + aa)$ families
$+ 48(Aa + aa)$ families
$+ 36(aa)$ families.

This is the fact.

In the next generation we shall have

$16\{36 + 1/4(48) + 1/16(80)\} = 16 \times 53 = 848AA$ families
$+ 16\{1/2(48) + 1/4(80)\} = 16 \times 44 = 704(AA + Aa)$ families
$+ 16\{1/8(80)\} = 160Aa$ families
$+ 16\{1/2(48) + 8 + 1/4(80)\} = 16 \times 52 = 832(AA + 2Aa + aa)$ families
$+ 704(Aa + aa)$ families
$+ 848aa$ families.

Succeeding generations follow the same law and need not be worked out in detail.

IV. So far the discussion has confined itself to families, as this must be the basic unit in the theory of any form of inbreeding. Turning to individuals we have the following simple relations to pass to individuals.

In the nth generation the number of

AA (or aa) individuals $= 2s(o_n) + s(p_n) + 1/2s(r_n)$,
Aa (or aA) individuals $= 2s(q_n) + s(1/2p_n) + 1/2s(r_n)$.

The first of the above expressions multiplied by 2 gives the total homozygotes, and the second multiplied by 2 gives the total heterozygotes.

RAYMOND PEARL

PARALLEL MUTATIONS IN ŒNOTHERA BIENNIS L.

In the summer of 1912 I cultivated pure strains of *O. biennis* L. and of the *O. biennis cruciata* de Vr. of our Dutch dunes, as well as of their hybrids, made with the purpose of studying the behavior of the *cruciata*-character in crosses. In one of these cultures I unexpectedly obtained two mutants, which because of their similarity to corresponding variants derived from *O. Lamarckiana* have been called *O. biennis nanella* and *O. biennis semi-gigas.* The first mutant, *O. biennis nanella,* occurred in the second generation of the cross *O. biennis* × *O. biennis cruciata* and differed from *O. biennis* in all those points which separate *O. Lamarckiana nanella* from *O. Lamarckiana.* The other variant, *O. biennis semi-gigas,* appeared in the second generation of the reciprocal cross, *O. biennis cruciata* × *O. biennis,* suggesting immediately by its much more vigorous habit and especially by the larger size of its buds and flowers the differences between *O. Lamarckiana* and *O. gigas.* A count of its diploid number of chromosomes proved it to deserve the name *semi-gigas,* 21 chromosomes being shown by nuclear plate-stages in the meristematic tissue of young buds. From these facts, showing that *O. biennis* is in a mutating condition, I drew the conclusion that the phenomenon of mutation in the genus *Œnothera* is older than the species *O. Lamarckiana*—*O. biennis* generally being considered to be an older species than *O. Lamarckiana*—and further, that the mutations in this group can not be the result of hybridization, as was assumed by some authors at that time—nobody doubting of the purity and constancy of *O. biennis.* As a matter of fact, both of my mutants have been derived from crosses between *O. biennis* and *O. biennis cruciata.* But I laid special emphasis on the fact that *O. biennis* and *O. biennis cruciata* have exactly the same germinal constitution except for the factors that determine the shape of the petals, *O. biennis cruciata* being prob-

ably a mutant from *O. biennis* itself. Therefore, hybrids between these two forms can be looked upon as pure *O. biennis* except for floral characters.

With this conception Bradley Moore Davis does not agree.[1] He thinks that the *O. biennis* and *O. biennis cruciata* of our dunes are not so closely related types, that a cross between them can be treated "as though it were the combination of forms within the same species which have similar germinal constitutions." He says:

> It should be made clear that the form "*O. biennis cruciata*" is recognized in the more recent taxonomic treatments as a true species sharply distinguished from types of *biennis* by its floral characters. . . . *O. cruciata* is found wild in certain regions of New England and New York and is consequently a native American species. . . . Whatever may have been the origin of *O. cruciata* or its possible relationship to *O. biennis*, a cross between these types must certainly be regarded as a cross between two very distinct evolutionary lines and its product a hybrid in which marked modifications of germinal constitution are to be expected.

From Davis's point of view I "really made a cross between two rather closely related species" and obtained in the second generation "two marked variants due to some germinal modifications as the result of the cross." In so far as my observations bear upon the problem of mutation Davis's interpretation is exactly the reverse of mine. To him they further illustrate the same phenomenon which he is obtaining through his "hybrids of *biennis* and *grandiflora*, namely, that behavior by which these hybrids in the F_2 generation throw off variants that in taxonomic practise would be considered new species readily distinguished from the parents of the cross and from the F_1 hybrid."

It will be shown in the following lines that the objections made by Davis are not sufficiently justified. My argument consists of two points.

In the first place, Davis is mistaken as to the nature of the *O. biennis cruciata* de Vr. of our dunes. This strain is in reality quite another type than the different forms of the American *O. cruciata* Nutt., called by some authors *O. biennis cruciata*. With this species it has in common only the character of the narrow

[1] Bradley Moore Davis, "Mutation in *Œnothera biennis* L.?" THE AMERICAN NATURALIST, Vol. XLVII, 1913, pp. 116–121; "Genetical Studies on *Œnothera*," IV, THE AMERICAN NATURALIST, Vol. XLVII, 1913, pp. 546–571.

petals, all other features of the stem, foliage, flowerspikes and fruits being exactly those of the Dutch *O. biennis* L. It must certainly be looked upon as a mutation from the *O. biennis* L. of our sand dunes. Until now it has only been found a couple of times in single individuals in the midst of the ordinary *O. biennis,* the first time in 1900 by Dr. Ernst de Vries in the dunes in the neighborhood of Santpoort, Holland, in one individual—and from this one specimen all the subsequent generations of *O. biennis cruciata* in the cultures grown by de Vries and by myself have been derived. Besides this, our *O. biennis* and *O. biennis cruciata* are so similar to one another except for floral structure that plants of both types can not be separated before the flowers open. Therefore we have the right to assume that the crossing of these two forms is concerned alone with the floral characters and that with respect to all other characters parents as well as hybrids are mere *biennis.* Therefore the two variants which arose in my cultures from crosses between *O. biennis* and *O. biennis cruciata* obviously prove the faculty of mutation in *O. biennis.*

In the second place I have found now that it is not necessary to cross *O. biennis* with *O. biennis cruciata* in order to obtain the above named mutants, as Davis seems to believe. Already in his new book Professor de Vries figures a dwarf derived from *O. biennis cruciata* grown in pure line. Shortly afterwards I myself obtained six mutants from the *O. biennis* of our sand dunes grown also in pure line. A few details about these cultures of last year may be given here. In all they counted 920 individuals, 430 of which belonged to the third and 490 to the fourth generation of a pure line, the point of departure for which had been one individual brought into the experimental garden in the rosette stage from the dunes near Wyk aan Zee in the beginning of 1905 and self-fertilized in the same year. The six mutants which appeared in these pure cultures of *O. biennis* were the following. First a dwarf, then a *biennis semi-gigas* having 21 chromosomes and finally four individuals of the *O. biennis sulfurea,* a pale-flowered form of *O. biennis,* which had been found already several times in our dunes in the midst of the ordinary *biennis,* but was not with certainty known to be a mutant from the latter form until now. The two first named mutants and one *sulfurea* appeared in the third generation of our pure line, the *nanella* and the *semi-gigas* coming from the same mother. The three remaining *sulfurea*-individuals appeared in the fourth generation, all

descending from the same motherplant. Of these mutants the *nanella* and *semi-gigas* are especially valuable because similar forms have been produced by *O. Lamarckiana.* It will be seen that the *biennis*-dwarfs seem to be somewhat rarer than the dwarfs of *Lamarckiana.* Whilst for the latter the mutation coefficient is about 1 per cent., our *O. biennis nanella* appeared as the only dwarf among 920 individuals. The above cited *O. biennis cruciata nanella* was the only dwarfed individual in a culture of 500. And the dwarf which I got in 1911 was the only one among about 600 plants. In this connection I wish to recall the conclusion reached by de Vries that in *O. Lamarckiana* the pangen for tall stature must be assumed to be present in the labile condition on both sides, in *O. biennis,* however, only in the male sexual type, whilst in the female sexual type active alta-pangens have to be supposed. The way from *biennis* to *biennis nanella* might therefore possibly be somewhat longer than the one from *Lamarckiana* to *Lamarckiana nanella.* The *biennis semi-gigas* which appeared in the last summer corresponded in all points exactly with the mutant of 1911. Moreover a count of the chromosomes, as shown by nuclear plate-stages in the meristematic tissue of young buds, determined them to be 21 in number. Even as the specimen of this type, that appeared in 1911, and as the *semi-gigas* mutants produced by *O. Lamarckiana,* the plant of last year proved to be almost absolutely sterile.

In his second above-mentioned paper Davis says about the *O. biennis* of our dunes: "No species of *Œnothera* is perhaps so free from suspicion as to its gametic purity. If Stomps can obtain mutations from tested material of the Dutch *biennis* grown in pure lines he will have the basis of a strong argument. . . ." Fortunately the experiment asked for by Davis, has been made in the same year as his criticism. The Dutch *biennis* L., cultivated in pure line, has produced a dwarf, a *semi-gigas* and some *sulfurea*-individuals, proving its mutability beyond all doubt. I therefore trust that the conclusions arrived at in my first paper, concerning this mutability and its consequences, may now be accepted as thoroughly valid.

Theo. J. Stomps

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IN a recent review[1] of Stomps's studies on *Œnothera biennis* L.[2] from the sand dunes of Holland I protested against his designating as mutants a *nanella* type and a *semi-gigas* type which were obtained in the second generation of crosses between *Œnothera biennis* Linnæus and its variety *O. biennis cruciata* de Vries. The criticism was presented on the general ground that however close the possible relationships between the two parent forms, they nevertheless constituted lines so far apart as to render unsafe a conclusion that marked variants obtained from their crossing are mutants in the sense of de Vries and Stomps. Such variants, it seemed to me, might have been the result of hybridism between two lines sufficiently divergent to upset the similarity of germinal constitution shown in their vegetative morphology, for the species *biennis* and its variety *cruciata* are said to differ only in their flower structure.

In that review I incorrectly associated *O. biennis cruciata* de Vries with *O. cruciata* Nutt., an American species entirely distinct from the variety *cruciata* of de Vries, which has been found only once (in the year 1900) on the sand dunes of Holland among plants of *O. biennis*. I greatly regret my confusion of these two types, since I was led in my criticism to regard Stomps's crosses between *biennis* and *biennis cruciata* as though they were crosses between two distinct although possibly closely related species. In this I was clearly mistaken, since all of the evidence short of experimental proof, which Stomps may yet obtain, indicates that *biennis cruciata* de Vries is a variety of *biennis* L. and arose as a mutation on the sand dunes of Holland. The crosses of Stomps are, therefore, to be regarded as between a species and its mutant variety. I trust that the mutationists will accept this acknowledgment of an error.

There is, I believe, a body of naturalists for whom the value of evidence for mutation rests fundamentally upon the unquestioned purity of the parent stock, and to them any cross, no matter how close, is open to criticism. Stomps has justified his first conclusions by obtaining in later studies the same mutants *biennis nanella* and *biennis semi-gigas* from lines of the pure species *O. biennis* Linnæus. Had he waited for these later results before

1 Davis, B. M., "Mutations in *Œnothera biennis* L.?" AMERICAN NATURALIST, Vol. XLVII, p. 116, 1913.

2 Stomps, T. J., "Mutation bei *Œnothera biennis* L.," *Biol. Centralb.*, Vol. XXXII, p. 521, 1912.

publishing on the first there could have been no objections to his main contention that *O. biennis* from the sand dunes of Holland is capable of giving rise to true mutants.

Stomps is continuing his studies on this same Dutch *biennis* with the view of determining its possible powers of mutation, and it is a pleasure to review his second paper[3] which presents some extremely interesting data, a paper in which no important criticism can be based on the source and character of the material employed. No wild species of evening primrose has been so long under experimental and field observation or is better known to the workers with œnotheras than this plant. The species has proved uniform in culture to a remarkable degree and it would be difficult to find a type of *Œnothera* so free from suspicion of gametic purity. The species appears to have been in Holland since pre-Linnæan days and is therefore very old. As material for experimental studies on mutation the Dutch *biennis* seems to the writer the best of all the œnotheras so far brought into the experimental garden.

The starting point of Stomps's cultures of *Œnothera biennis* was a plant transplanted from the sand dunes in 1905. From seed of this plant, self-pollinated, a second generation was grown in 1910, three selfed plants of which gave the seed for a third generation of 430 individuals, and a fourth generation of 490 plants was grown from two selfed plants of the third generation. Thus in all 930 individuals were observed in the third and fourth generations from the plant that gave rise to these pure lines. It is true that these lines have not been under selection for many generations, but, considering the stability of the species and its habit of close pollination, it is very improbable that the source of the cultures should have been a plant not representative of the type. Furthermore, Stomps presumably will continue indefinitely the lines now established and thus determine through later generations whether their mutating habits remain constant.

Among the 430 plants of the third generation there appeared 1 *biennis nanella*, 1 *biennis semi-gigas* and 1 individual of *biennis sulfurea;* the first two came from the same mother plant. Among the 490 plants of the fourth generation appeared 3 individuals of *biennis sulfurea,* all from the same selfed mother. The variety *sulfurea* differs from the species *biennis* in having flowers of a

[3] Stomps, T. J., "Parallele Mutationen bei *Œnothera biennis* L.," *Ber. deut. bot. Gesell.,* Vol. XXXII, p. 179, 1914.

lighter yellow, and is reported by de Vries to be not uncommon in the wild state mixed with the species proper. *Sulfurea* has been held systematically to be a variety of *biennis* but this is the first time that it has appeared in the experimental garden as a derivative of that species. Thus out of a total of 920 plants there were 4 individuals of the color variety *sulfurea,* 1 *nanella* and 1 *semi-gigas,* in all 6 mutants, a showing that may well gratify Stomps.

The mutant *biennis nanella* differed from typical *biennis* in much the same way that *Lamarckiana nanella* differs from *Lamarckiana* and like the latter dwarf showed evidence of a bacterial infection. Certain selfed flowers set no seed because of diseased stigmas. Other flowers pollinated from pure *biennis* set good fruit. The ratio of the appearance of *biennis nanella* is much lower than the mutation coefficient of one per cent. which de Vries has reported for *Lamarckiana nanella.* It should also be remembered that de Vries[4] obtained a *cruciata nanella* in a culture of 500 plants from *O. biennis cruciata.*

The mutant *biennis semi-gigas* in comparison with typical *biennis* showed a stronger habit, broader leaves, thicker buds, larger flowers, supernumerary stigma lobes, and the presence of 4-cornered pollen grains. Counts of the chromosomes in meristematic tissue determined the number to be 21. Therefore in this plant, as in the *biennis semi-gigas* obtained by Stomps from the cross *cruciata* × *biennis,* there is clear cytological evidence that one of the gametes which formed the zygote contained 14 chromosomes, *i. e.,* double the number characteristic of the gametes of *Œnothera.* This is another case of triploid mutants in *Œnothera* to be added to the list of Stomps and Miss Lutz. The plant was self sterile, but set fruit when pollinated by *biennis,* although the yield of seed was very poor.

Stomps is justified in calling attention to the agreement of his second *biennis nanella* with the plant derived in 1911 from the cross *biennis* × *cruciata,* and of the agreement of his second *biennis semi-gigas* with the plant from the cross *cruciata* × *biennis.* It is to be hoped that he will next obtain the *cruciata* variety as a direct mutant from the Dutch *biennis* and thus establish its relationship and origin beyond all possible doubt.

Stomps has before him the opportunity of making through the study of *Œnothera biennis* very important contributions to our

[4] See "Gruppenweise Artbildung," p. 299 and Fig. 108.

knowledge of the frequency of mutations and their importance in organic evolution. That retrogressive mutations take place is not likely to be seriously doubted by any one who has followed the experimental work of recent years both botanical and zoological. The loss of characters through germinal modification, even in what seem to be "pure lines," appears to be not uncommon.

Most of all is desired information on the possibilities, frequency and character of progressive mutations. Can the mutation theory satisfactorily explain progressive advances in organic evolution or must amphimixis chiefly carry that responsibility? Mutants of the tetraploid *gigas*-like type would appear to be progressive, and we can see the reason in their doubled chromosome count which gives larger nuclei, larger cells and modified tissues. *Gigas*-like forms are however very rare and in *O. Lamarckiana gigas* the fertility is relatively low. More common are the triploid *semi-gigas* forms, but these seem to be sterile or almost sterile when selfed, and the work of Geerts indicates that the triploid number in *Œnothera* returns to the normal through the elimination of supernumerary chromosomes. Very interesting is the recent paper of Gates and Thomas[5] which offers evidence that *lata*-like characters are associated with the presence of a single additional chromosome.

And what of the series of forms which differ from the *Œnothera* parent types with as yet no evidence of peculiarities in their chromosome count, *brevistylis, lævifolia, rubrinervis, obovata, scintillans,* etc. Will forms similar to these and perhaps others in addition be represented in a series of derivatives from *Œnothera biennis?* The mutants *biennis nanella* and *biennis sulfurea* belong to this group and have already been obtained by Stomps. One may almost envy him his opportunity for an intensive study of this species.

Bradley Moore Davis

University of Pennsylvania,
June, 1914.

[5] Gates, R. R., and Thomas, N., "A Cytological Study of *Œnothera* mut. *lata* and *Œ.* mut. *semilata* in Relation to Mutation," *Quart. Jour. Mic. Sci.*, Vol. LIX, p. 523, 1914.

THE THEORETICAL DISTINCTION BETWEEN MULTIPLE ALLELOMORPHS AND CLOSE LINKAGE

PROFESSOR CASTLE's difficulty in understanding the distinction made by Mr. Dexter[1] is owing to his unfamiliarity at first hand with the phenomenon of linkage. The distinction between allelomorphs and close linkage has already been given several times elsewhere and need not be repeated; but if Professor Castle has failed to note it, or to see its significance, it is probable that others may have done the same. I may be pardoned, therefore, for attempting once more to show why, for clear thinking, it is important to keep in mind the difference between allelomorphs and close linkage. Furthermore, since we have here one of the newest developments of Mendelism, it seems to me that it may be worth while not to let Professor Castle's criticism pass unchallenged.

Dexter pointed out that the mode of treatment that Nabours followed in the analysis of his results is the procedure of multiple allelomorphism, although Nabours does not seem entirely conversant with the fact, but treats the results as though they were regular phenomena. In one case, however, Nabours got an unconformable individual. Dexter points out that if this case is not due to non-disjunction (a known process that will cover such cases) it shows that here at least the factors involved are not allelomorphs, but must be treated as though closely linked.

How could the matter be put more directly? I confess I am at somewhat of a loss to discover why Professor Castle is confused. Perhaps it is the subsequent development of Dexter's explanation that has troubled him. Let us again try to make the distinction clear.

If the factors B and E are not allelomorphic to each other then each must have another allelomorph. This is nothing but pure Mendelism, which no one will, I suppose, dispute. It is entirely irrelevant whether we use small letters or none at all (as Castle prefers) for the allelomorphs. If they are a part of the Mendelian machinery, who cares very much what we call them?

If then we have here two pairs of allelomorphs, crossing over may take place, as it does in other cases where two pairs of linked

[1] THE AMERICAN NATURALIST, June, 1914, p. 383.

genes are involved.[2] This is all there is to the matter. We need not dwell, therefore, at length on Professor Castle's statement that here is another case of an erroneous conclusion reached in consequence of using small letters for "absent" characters, except to remark that Dexter did not use small letters for absent characters, and that the erroneous conclusion has been drawn by Professor Castle himself.

T. H. Morgan

Columbia University

Professor Morgan has called my attention to the fact that in criticizing a single point in Mr. Dexter's review I have given the impression, to some at least, that I regarded Dexter's views as erroneous. Such was not my intention, and I wish to correct the impression, if I may. I do not for a moment question the reality of "unit-character" inheritance or indorse the idea of "the organism as a whole" as the only inheritance unit. I agree here entirely with the view which I understand Dexter to hold. If Nabours has encountered nothing but simple allelomorphs among his grasshoppers (which I neither assert nor deny), this by no means proves that only simple allelomorphs exist even among said grasshoppers. An organism which seems to have only one variable "gene" may nevertheless possess any number of other genes which are not varying so far as we can discover, and in which consequently all zygotes are homozygous and all gametes similar to each other.

It is only in Dexter's discussion of the significance of the exceptional "*B E I*" individual that I should dissent from any part of his excellent review. Nabours's explanation of this case, according to Dexter, is essentially that of "non-disjunction," instead of which Dexter himself offers the explanation of "linkage," and proposes a repetition of the experiment to decide between them. Now I do not question for a moment the genuineness of either "non-disjunction" or "linkage," as they occur for example in *Drosophila*. Through the kindness of Professor Morgan I have been able to demonstrate both these phenomena repeatedly to classes in genetics in the course of their laboratory work upon *Drosophila*. The point which I wished to make in com-

[2] Crossing over would not take place if the factors in question were allelomorphic. If the case is one of non-disjunction the subsequent generation would also give a different kind of result from that of linkage. (See Bridges, *Jour. Exp. Zool.*, 1913.)

menting on Dexter's review (and this is the *only* point in which I dissent from his opinions) is that the repetition of the experiment, provided it had the outcome suggested by Dexter, would leave us as much in the dark as we were before concerning the correct interpretation of the result. Very likely, however, *additional* facts might be observed which *would* give some clue, so that I quite agree with Dexter's suggestion that the case should receive further study. But I can not see that *at present* linkage has more in its favor as an interpretation than non-disjunction.

The "demonstration" which Mr. Dexter gave of his argument by introducing duplicate "symbols" instead of the single set used by Nabours, seemed to me quite superfluous and possibly to have been a real stumbling block in the logical process. This is why I raised the question as to the significance of the small letters. The terminology is that of the "presence-absence" hypothesis, as commonly understood, but Professor Morgan assures me that such is not the significance which Dexter attaches to the symbols used. It seems to me therefore that the significance attached to the symbols is vital to the argument in the "demonstration."

I quite agree with Professor Morgan, however, that symbols are a matter of small consequence. Suppose we omit the "demonstration" by means of symbols altogether. Should we then have any reason to favor linkage as an interpretation rather than non-disjunction? I can not see that we should have. It seems to me quite possible that neither explanation will prove adequate.

When albino mammals are crossed with colored ones, piebalds sometimes are obtained in later generations. So far as we know, these result neither from "non-disjunction" nor from "crossovers." Perhaps the *B E I* individual also is a *tertium quid*.

W. E. CASTLE

NOTES AND LITERATURE

BIOMETRICS

An Important Contribution to Statistical Theory

One of Pearson's most valuable contributions to statistical theory is his test for goodness of fit.[1] It enables one, with the aid of Elderton's[2] tables, easily to determine the probability that a given system of observed frequencies does or does not differ significantly from a series of theoretical frequencies supposed to graduate the observations. The significance of this criterion in Mendelian work has recently been pointed out by Harris.[3]

Hitherto this criterion has found an important limitation in the fact that, as originally developed by Pearson, it was applicable only to frequency systems. It could be used to test goodness of fit only where the observations were counts of the number of times particular classes of events occurred. But, of course, frequency systems comprise only one kind of observational data to which one has occasion to fit curves. Much more often there is need for a criterion of goodness of fit where the observations are of the nature of true ordinates, rather than frequencies. Such cases include all data of the sort where a mean y is determined for each x, as in a growth curve; or in the regression observed in a correlation table, where for each successive value of one of the variables the mean value of the correlated variable is calculated. There has been no method of testing the goodness of fit for such curves. From a visual inspection of the plotted regression line one has been compelled to form his judgment as to whether it was or was not a good fit.

Recently a Russian statistician, E. Slutsky,[4] has extended

[1] Pearson, K., "On the Criterion that a Given System of Deviation from the Probable in the Case of a Correlated System of Variables is Such that it Can be Reasonably Supposed to Have Arisen from Random Sampling," *Phil. Mag.*, 5th Series, Vol. L, pp. 157–175, 1900.

[2] *Biometrika*, Vol. I, pp. 155–163.

[3] Harris, J. A., "A Simple Test of the Goodness of Fit of Mendelian Ratios," Amer. Nat., Vol. 46, 1912, pp. 741–745, 1912.

[4] Slutsky, E., "On the Criterion of Goodness of Fit of the Regression Lines and on the Best Method of Fitting Them to the Data," *Jour. Roy. Stat. Soc.*, Vol. LXXVII, Part I (December, 1913), issued 1914, pp. 78–84.

Pearson's theory to cover the class of curves, formerly not amenable to such test. The result forms an extremely valuable extension of biometric theory.

Briefly Slutsky's essential result may be put as follows. He finds (the complete proof is not given in this paper) that

$$\chi^2 = S\left(\frac{n_{x_p} e_p^2}{\sigma_{n_{x_p}}^2}\right),$$

where χ^2 is the quantity denoted by the same letter in Pearson's original work, and is the argument in Elderton's table; n_{x_p} is the frequency in the x_p array, *i. e.*, the number of observations on which each observed ordinate is based; e_p is the difference between the observed and the calculated mean y for each x_p array; and $\sigma_{n_{x_p}}$ is the standard deviation of each x_p array; *i. e.*, the standard deviation of the group of observations from which each particular y was calculated. S, as usual, denotes summation. Knowing χ^2, P is read directly from Elderton's tables.

Slutsky gives a couple of examples of the application of the method in his paper. For illustration here I have preferred to take an example from my own unpublished data. The observations (y_{x_p}) in this case are the mean butter productions of American Jersey cattle, based on seven-day tests.[5]

The theoretical points Y_{x_p} are calculated from the equation,

$$y = 14.21098 + .0250x - .0038x^2 + 3.0104 \log x,$$

the constants of which were determined from the observations by the method of least squares.

The test for goodness of fit is carried out in Table I. It should be said that, following the suggestion given by Slutsky in his paper, I have used in the $\sigma_{n_{x_p}}$ column the graduated rather than the observed values. In the present case the scedastic curve is hopelessly far from a straight line. It is, in point of fact, logarithmic.

From this table we have $\chi^2 = 32.115$. This is beyond the range of Elderton's table. By a rough, but sufficiently accurate, graphical extrapolation, I find for present values of n' and χ^2,

$$P = .417 \text{ about.}$$

In other words, if the butter production of Jersey cows changes with age according to the curve given, we should expect to

[5] For data see "Jersey Sires and Their Tested Daughters," published by American Jersey Cattle Club, New York, 1909.

get a worse agreement between observation and theory in 42 out of every 100 random samples on which the point was tested. In other words, the fit may be considered sufficiently good. As a matter of fact, the fit is extraordinarily close over most of the curve. Four (only) out of the 32 ordinates contribute more than 50 per cent. of the value of χ^2.

TABLE I

Age in Years	Observed Butter Production in Lbs.	Calc. Butter Production in Lbs.	Errors	Frequency	Standard Dev. of Arrays	
x_p	y_{x_p}	Y_{x_p}	$e_p = (Y_{x_p} - y_{x_p})$	n_{x_p}	$\sigma_{n_{x_p}}$	$\frac{n_{x_p} e_p^2}{\sigma^2_{n_{x_p}}}$
1.25	14.25	14.23	.02	2	.04	.500
1.75	15.15	15.15	.00	46	.97	.000
2.25	15.57	15.69	.12	273	1.49	1.771
2.75	15.96	16.06	.10	312	1.83	.932
3.25	16.38	16.35	.03	545	2.07	.114
3.75	16.72	16.57	.15	511	2.25	2.271
4.25	16.92	16.74	.18	704	2.38	4.027
4.75	17.09	16.89	.20	532	2.49	3.432
5.25	17.01	17.00	.01	556	2.56	.008
5.75	17.07	17.09	.02	382	2.62	.022
6.25	16.98	17.16	.18	419	2.65	1.933
6.75	17.04	17.21	.17	277	2.68	1.114
7.25	17.09	17.25	.16	285	2.68	1.016
7.75	17.48	17.27	.21	190	2.68	1.167
8.25	17.30	17.28	.02	166	2.67	.009
8.75	17.17	17.27	.10	121	2.64	.174
9.25	17.56	17.25	.31	109	2.61	1.515
9.75	16.67	17.21	.54	95	2.57	4.194
10.25	17.05	17.17	.12	63	2.52	.143
10.75	17.42	17.11	.31	39	2.46	.619
11.25	16.95	17.05	.10	54	2.40	.094
11.75	17.00	16.97	.03	28	2.33	.005
12.25	17.05	16.88	.17	20	2.26	.113
12.75	16.54	16.79	.25	7	2.18	.092
13.25	16.34	16.68	.34	11	2.09	.291
13.75	18.14	16.56	1.58	9	1.99	5.673
14.25	15.89	16.44	.55	7	1.88	.599
14.75	16.15	16.30	.15	5	1.77	.036
15.25	16.37	16.16	.21	4	1.65	.065
15.75	15.75	16.00	.25	2	1.53	.053
16.25	15.42	15.84	.42	3	1.40	.117
16.75	15.75	15.67	.08	4	1.27	.016
Totals ...				5,781		32.115

It may be said, in conclusion, that Slutsky's contribution is one which will be highly valued by all investigators who have a critical interest in the graduation of observational data, whatever the field in which they may be working.

RAYMOND PEARL

A NEW MODE OF SEGREGATION IN GREGORY'S TETRAPLOID PRIMULAS

In a recent paper[1] Gregory reports a very interesting case in which two different races of *Primulas* suddenly gave rise to giant tetraploid forms, having double the usual number of chromosomes, and apparently having the factors doubled also (individually), for this was true of all the factors which could be followed in his hybridization experiments. It is important to know how segregation will take place in such individuals, as there are four allelomorphs of each gene present.

Let us suppose that a tetraploid form pure for the dominant factor A $\left(\text{and therefore of composition } \frac{A\ A}{A\ A}\right)$ is crossed with a pure recessive giant $\left(\frac{a\ a}{a\ a}\right)$. Gametes AA and aa will meet in fertilization, forming the hybrid $\frac{A\ A}{a\ a}$ (the maternally derived genes are represented on one line, say the upper, the paternally derived genes on the other line).

Now, if this were an ordinary case of "multiple factors"[2] in a diploid organism, although the two dominant factors, which we may again call A's, may produce the same effect upon the organism, yet they are not interchangeable, and the same is true of the recessive factors. That is, if we call both dominants A, we must designate one of them as A^1, and the corresponding recessives must also be designated as a and a^1, for A will always segregate into a different gamete from a, and A^1 from a^1, there being two distinct allelomorphic pairs. On the chromosome view of heredity, we would say that A and a always lay opposed to each other, in homologous chromosomes, on the spindle of the reduction division, as did also A^1 and a^1, but neither A nor a lay in chromosomes homologous to those of either A^1 or a^1, and assorted independently of them. The line-up of factors on the spindle in the reduction division in this case would be equally likely to be $\frac{A\ A^1}{a\ a^1}$ or $\frac{A\ a^1}{a\ A^1}$, depending merely upon which

[1] R. P. Gregory, "On the Genetics of Tetraploid Plants in *Primula sinensis*," *Proceedings of the Royal Society*, 1914.

[2] *i. e.*, a case where two (or more) independent pairs of factors produce similar effects, upon the same character. Many examples of this are known, *e. g.*, the inheritance of red flower in flax.

way the pairs are turned with reference to each other. The first alignment gives gametes AA^1 and aa^1, the second gives Aa^1 and aA^1. Thus three gametes with a dominant factor to one pure recessive would on the average be produced, the ratio being 1AA : 2Aa : 1aa, omitting primes.

In a tetraploid form, however, A and A^1 are alike and interchangeable, as also are a and a^1. In the hybrid $\frac{A}{a}\frac{A^1}{a^1}$, therefore, there would be at least one other mode of pairing of allelomorphs possible, giving two new modes of line-up on the reduction spindle, and they would occur just as frequently as the two previous kinds. The two new arrangements would be $\frac{A}{a^1}\frac{A^1}{a}$, giving gametes AA^1 and a^1a, like those in the first of the two previous cases, and $\frac{A}{a^1}\frac{a}{A^1}$, giving gametes Aa and a^1A^1.[3] These latter gametes would be indistinguishable from the Aa^1 and aA^1 gametes given by the second of the two usual arrangements unless A could be distinguished from A^1 and a from a^1. This could happen only if the allelomorphs were of four different kinds or if there were linkage of these genes with other genes for which the plant was heterozygous. Unless, therefore, linkage or multiple allelomorphism were involved, we could not distinguish between this mode of pairing of allelomorphs and the usual kind; both would give three gametes containing at least one dominant to one pure recessive (*i. e.*, 1AA : 2Aa : 1aa, omitting primes).

Still a third type of pairing of allelomorphs is possible in a tetraploid plant, however. There seems no *a priori* reason, on the chromosome view, why, in a tetraploid plant, a gene should have to segregate from one of the allelomorphs derived from the opposite parent. That is, in a plant of composition $\frac{A}{a}\frac{A^1}{a^1}$, paternally derived genes being indicated on, say, the upper line, maternally derived ones on the lower, there is no apparent reason why the line-up of chromosomes at reduction should not be $\frac{A}{A^1}\frac{a}{a^1}$ $\frac{A}{A^1}\frac{a^1}{a}$ or as often as it is one of the other types, since all four chromosomes are homologous. Thus we should get gametes Aa, A^1a^1, Aa^1 and A^1a.

[3] If linkage with other genes could be followed, we should with this mode of pairing obtain crossing over between the chromosomes containing A and a^1, respectively, and between those containing A^1 and a, respectively; this would not occur on any other mode of pairing.

We could distinguish such gametes individually from those obtained by the ordinary arrangements only if linkage were involved, for then we should sometimes obtain results indicating that the chromosomes containing A and A^1 had crossed over with one another, and so had probably behaved as homologous chromosomes at the reduction division. However, we could also determine whether this mode of pairing occurred or not merely by determining the relative numbers of the different kinds of gametes formed. For, if the third type of pairing occurred, we should obtain 4Aa gametes in addition to the 2AA, 4Aa and 2aa derived from the other two types of pairing. The ratio of gametes would then be five containing a dominant to one recessive, there being 1AA : 4Aa : 1aa, as opposed to the ratio 1AA : 2Aa : 1aa obtainable on either of the other modes of segregation.[4] The latter or more usual ratio is the only one considered by Gregory, who apparently takes it for granted that in so far segregation must be of the same sort as in diploid forms.

Let us see which ratio is more in accord with his experimental data. As the ratio of offspring in a back-cross is the same as the gametic ratio, it will be seen that a back-cross of $\frac{A}{a}\frac{A}{a}$ by a recessive should give 3A : 1a plant on Gregory's view, the 3A's consisting of $1\frac{A}{a}\frac{A}{a} : 2\frac{A}{a}\frac{a}{a}$. On the other view, a back-cross should result in 5A : 1a, the 5A's consisting of $1\frac{A}{a}\frac{A}{a} : 4\frac{A}{a}\frac{a}{a}$. On inbreeding an $\frac{A}{a}\frac{A}{a}$ plant, however, owing to the random fertilization of gametes, Gregory's 3 : 1 gametic ratio would result in a 15 : 1 ratio among the offspring (which correspond to F_2) and our own 5 : 1 gametic ratio would give a 35 : 1 ratio of A to a among the offspring.

A summary of his back-crosses of P_1 heterozygous thrum-eyed plants of the type $\frac{A}{a}\frac{A}{a}$ to recessive pin-eyed plants $\frac{a}{a}\frac{a}{a}$ gives the result 61 thrum : 6 pin (10 : 1, as compared to the two expectations 3 : 1 and 5 : 1). Among the F_1 thrums there should

[4] Counts of chromosomes in the maturation divisions of the tetraploid plants show that the chromosomes synapsed in pairs, not in groups of four. Synapsis in fours would be, in effect, the same as pairing of the random sort suggested in this paper, so far as any one set of allelomorphs are concerned, but it might give different linkage results.

on Gregory's view be $1\frac{A}{a}\frac{A}{a}:2\frac{A}{a}\frac{a}{a}$, on the other view $1\frac{A}{a}\frac{A}{a}:4\frac{A}{a}\frac{a}{a}$. Tests of twenty-one F_1 thrums, by mating them to themselves and also to recessives, showed that there was only one which was certainly $\frac{A}{a}\frac{A}{a}$ and 15 which must have been $\frac{A}{a}\frac{a}{a}$. (A few gave numbers too small to be significant, and one or two were of doubtful composition.) This result is within the limits of probable error on the 4:1, but hardly on the 2:1 expectation. The one F_1 thrum plant which was of composition $\frac{A}{a}\frac{A}{a}$ gave, on back-crossing, 67 thrums: 18 pins, a ratio of 3.7:1, to correspond with Gregory's 3:1 or my 5:1 expectation. On inbreeding it gave 44 thrums: 2 pins, a ratio of 22:1, to correspond with Gregory's 15:1 or my 35:1 expectation. The other F_1 thrums, being of composition $\frac{A}{a}\frac{a}{a}$ (aside from the few doubtful ones), gave, on the average, 1 thrum: 1 pin on back-crossing, and 3 thrums: 1 pin on inbreeding; these results would be expected on either view.

Crosses were also made involving the character green versus red stigma (green being dominant). Here the $\frac{A}{a}\frac{A}{a}$ forms, on back-crossing, gave a total of 114 green: 30 red (3.8:1 instead of 3:1 or 5:1), and on inbreeding they gave 75 green: 2 red (37.5:1 instead of 15:1, as on Gregory's expectation, or 35:1, on my own).

It will be seen that the numbers in the above crosses are too small to be very significant, individually, for a settlement of the question at issue, but if summed up they become more decisive. Thus, a summary of the offspring of all back-crosses of the $\frac{A}{a}\frac{A}{a}$ form to the recessive gives 242 dominants (A): 54 recessives (a), or 4.5:1, as compared with the 3:1 expectation of Gregory and the 5:1 of the view advocated in this paper. Where the dominants among these offspring were tested they were found to consist of $1\frac{A}{a}\frac{a}{a}$ and $15\frac{A}{a}\frac{A}{a}$, as compared with the 1:2 expectation of Gregory, and ours of 1:4. Finally, a summary of the cases where $\frac{A}{a}\frac{A}{a}$ forms were inbred shows that 119 dominants: 4 recessives resulted, a ratio of 30:1 where Greg-

ory's expectation would be 15:1 and our own 35:1. Moreover, the individual records fluctuate in both directions about the ratios to be expected upon our point of view, but practically all vary in the same direction from the expectation of Gregory, namely, in the direction of the other expectation.

There is reason, then, to believe that in these *Primulas* the factors derived from the same parents may segregate from each other as allelomorphs, while allelomorphs derived from opposite parents meanwhile assort at random. For although the allelomorphs exist in sets of four they must pair two by two for segregation, as do the chromosomes, and two derived from the same parent may happen to pair with one another. The chance that this should occur is one third, since there are three possible modes of pairing. Such a result is difficult to explain except on the chromosome view of heredity. It would give ratios different from those theoretically expected by Gregory, but more in accord with his experimental data. The principle upon which our own expectation is founded may be briefly summed up by saying that where more than two factors which are normally allelomorphic to each other are present, the pairing of these allelomorphs with each other preparatory to segregation usually[5] takes place at random.

HERMANN J. MULLER

[5] That this is not always true is shown by Bridges' case of "non-disjunctional" females of *Drosophila*, which contain one Y and two X chromosomes. Any two of these chromosomes normally act as homologues to each other in the reduction division of the normal fly, which contains only two of them. But where all three are present together they do not pair at random, for they oftener undergo the segregation X–XY than XX–Y, presumably because the two X's are much more like each other than like the Y, and so more apt to act as homologues.

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STUDIES ON INBREEDING. V

Inbreeding and Relationship Coefficients[1]

Dr. RAYMOND PEARL

University of Maine

In the discussion of inbreeding coefficients contained in a series of recent papers from this laboratory[2] no mention has been made of an important consideration which arises in connection with such coefficients. The further problem, to which we may now turn, may be stated in the following way.

The pedigree of an individual consists of two halves. One of these halves is made up of the sire and his ancestors; the other of the dam and her ancestors. Following the conception of inbreeding set forth in detail in the earlier papers of this series it is plain that the values of the coefficients of inbreeding for a particular pedigree are composed of the following elements.

1. The occurrence of the same individual animals more than once on the sire's side of the pedigree only.

2. The occurrence of the same individual animals more than once on the dam's side of the pedigree only.

[1] Papers from the Biological Laboratory of the Maine Agricultural Experiment Station, No. 69.

[2] Pearl, R., "Studies on Inbreeding. I. A Contribution Towards an Analysis of the Problem of Inbreeding," Amer. Nat., Vol. XLVII, pp. 577–614, 1913; "The Measurement of the Intensity of Inbreeding," *Me. Agr. Expt. Sta. Bul.*, 215, pp. 123–138, 1913. Pearl, R., and Miner, J. R., "Studies on Inbreeding. III. Tables for Calculating Coefficients of Inbreeding," Me. Agr. Expt. Sta. Ann. Rept. for 1913, pp. 191–202, 1913.

3. The reappearance of animals which appear first on one side of the pedigree (either the sire's or the dam's) on the other side.

If only 1 and 2 are to be found in the pedigree it means that the sire and the dam are totally unrelated (within the limits covered by the pedigree in the particular case). On the other hand, the occurrence of 3 means that sire and dam are in some degree related, and that a portion of the observed inbreeding arises because of that fact. Now the coefficients of inbreeding, in and of themselves, tell nothing about what proportionate part has been played by these three elements in reaching the final result. It is a matter of great importance to have information on this point, because of its genetic significance. It is the purpose of this paper to describe a general method for obtaining this desired information.

The first step in the method, stated briefly, is to break up the pedigree elimination table formed to get the successive values of $p_{n+1} - q_{n+1}$, in our former notation, into four different parts. One of these parts will include the primary reappearance on the sire's side of the pedigree of such animals as appear first on the same side. This may be called the "male only" table. The second part will include the primary reappearance on the dam's side of such animals as first appear on the same side. This is the "female only" table. The third part will include the primary reappearance on the dam's side of such animals as first appear on the sire's side. The fourth part is the reverse of the third. These last two may be called the "cross tables." The sums of the totals of these partial tables will give the total $p_{n+1} - q_{n+1}$ values for the successive generations.

The formation of the tables on this plan may be illustrated with some examples. These examples will also show the skeleton method of writing pedigree elimination tables, which saves much labor. This was referred to, but not significantly illustrated, in the earlier papers. It consists simply in doubling the total of the column for each generation rather than the separate items.

TABLE I

Partial Pedigree Elimination Table for King Melia Rioter 14th Showing the Primary Reappearances on the Sire's Side of the Pedigree of Animals which First Appear on that Side

Generation	2	3	4	5	6	7	8	9	10	11	12
Melia Ann's Son			1	(2)[3]							
Melia Ann 3d				1	(6)[3]						
Lucy's Stoke Pogis					3						
Melia Ann					2						
St. Lambert Boy					1						
Letty Rioter					1						
Allie of St. Lambert					1						
Lord Aylmer					1						
Amelia 2d					1	(32)[3]					
Victor Hugo						1					
Oakland's Nora						1					
Stoke Pogis 3d						1					
Bachelor of St. Lambert						1					
Sir George of St. Lambert						1					
Diana's Rioter						1					
Orloff						1					
Lorne						1					
Hugo's Victoria						1	(82)[3]				
Victor Hugo							1				
Pauline							1				
Canada's John Bull							1				
Oakland's Nora							1				
Stoke Pogis 3d							7				
Kathleen of St. Lambert							1				
Lord Lisgar							4				
Lucy of St. Lambert							2				
Diana of St. Lambert							1				
Pet of St. Lambert							1				
Orloff							1				
Bachelor of St. Lambert							1				
Ida of St. Lambert							1	(210)[3]			
Victor Hugo								2			
Stoke Pogis 3d								2			
Lord Lisgar								3			
Lorne								1			
Amelia								1	(438)[3]		
Lord Lisgar									1		
Pride of Windsor									2		
Laval									1		
Amelia									2		
Victor Hugo									3	(894)[3]	
Laval										1	
Amelia										1	
Lisette										1	
Berthe										1	
Totals			1	3	16	41	105	219	447	898	1,796

[3] In this and the following table the numbers in brackets are in each case twice the sum of the numbers in the preceding column. They represent the accumulated ancestral reduplication up to the generation in question.

The pedigree for 12 ancestral generations of the Jersey bull King Melia Rioter 14th (103901) may be taken as the first illustration.

TABLE II

PARTIAL PEDIGREE ELIMINATION TABLE FOR KING MELIA RIOTER 14TH SHOWING THE PRIMARY REAPPEARANCES ON THE DAM'S SIDE OF THE PEDIGREE OF ANIMALS WHICH FIRST APPEAR ON THAT SIDE

Generation	2	3	4	5	6	7	8	9	10	11	12
King's Rioter Lad	—	—	—	1	2	4	8	16	32	64	128

Table III is clearly the one which demands special attention. As will shortly appear, it is the most important for the theory of inbreeding. Let us attempt its analysis. Just what does the first entry mean genetically? It states that King Melia Rioter, an animal which first appeared on the sire's side of the pedigree, reappeared in the second ancestral generation on the dam's side. What this clearly means is that at least one half of all the dam's ancestors, in the third and higher ancestral generations, *are identically the same animals as are ancestors of the*

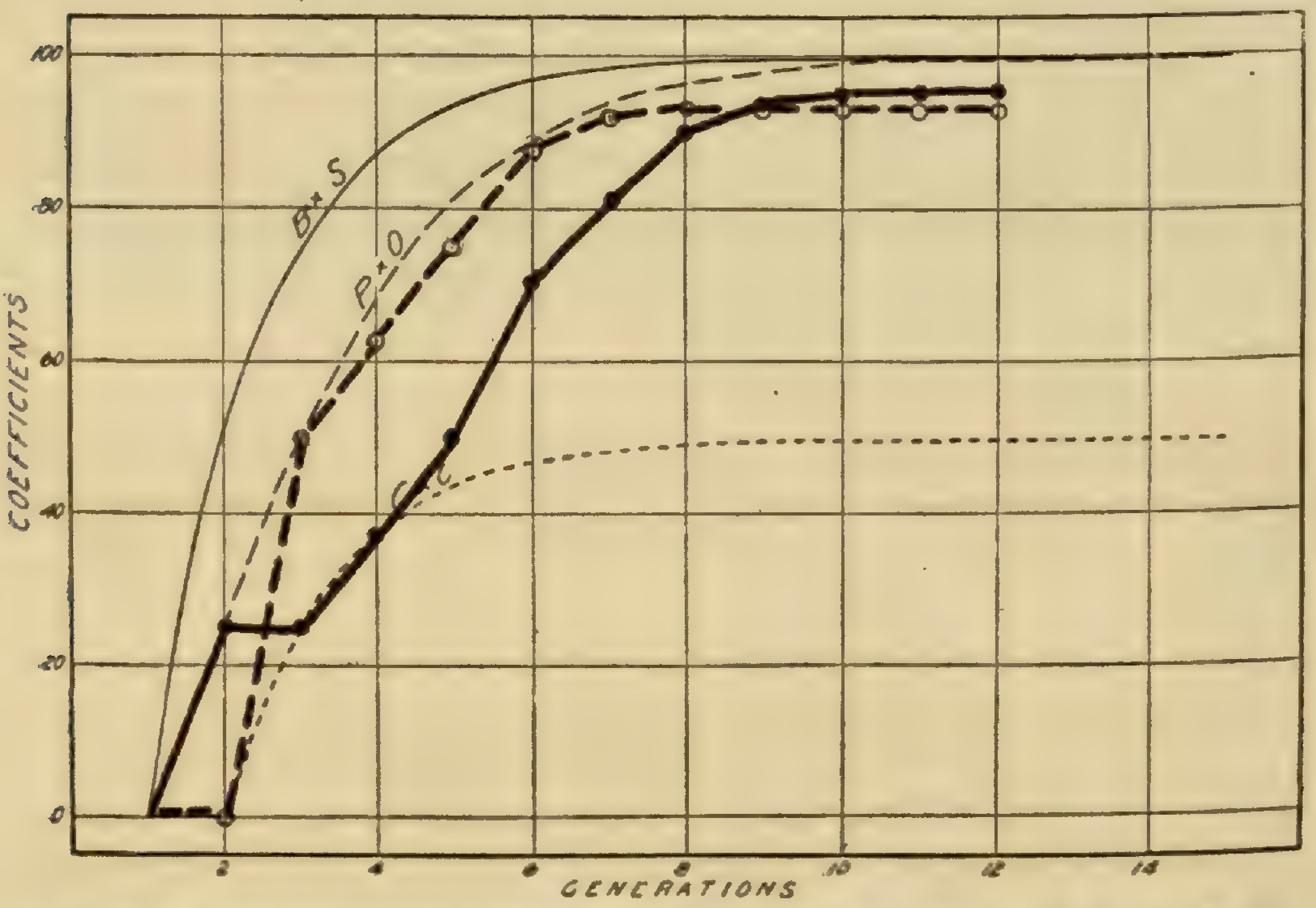

FIG. 1. Diagram showing (*a*) the total inbreeding (heavy solid line) and (*b*) the relationship (heavy broken line) curves for the Jersey bull, King Melia Rioter 14th. The high order of the inbreeding and relationship between the sire and dam in this case is evident by comparison with the lighter lines, which give the maximum values for continued brother × sister, parent × offspring and cousin × cousin breeding.

sire. The next entry in Table III indicates that in the fourth and higher ancestral generations at least 5/8 of all the dam's ancestors were the same individual animals as were also ancestors of the sire. One half of them were the same before the reappearance of St. Lambert's Rioter King. He makes up the additional 1/8 of the dam's ancestry.

TABLE III

PARTIAL PEDIGREE ELIMINATION TABLE FOR KING MELIA RIOTER 14TH SHOWING THE PRIMARY REAPPEARANCES ON THE DAM'S SIDE OF THE PEDIGREE OF ANIMALS WHICH FIRST APPEAR ON THE SIRE'S SIDE

Generation	2	3	4	5	6	7	8	9	10	11	12
King Melia Rioter	1	(2)	(4)								
St. Lambert's Rioter King			1	(10)							
King of St. Lambert				1							
St. Lambert Boy				1	(24)						
St. Lambert Boy					2						
Oakland's Nora					1						
St. Lambert's Rioter King					1	(56)					
St. Lambert Boy						1					
King of St. Lambert						1					
St. Lambert's Letty						1	(118)				
Letty Coles 2d							1	(238)			
King of St. Lambert								1			
Louise's Grace								1			
Totals	1	2	5	12	28	59	119	240	480	960	1,920

From these tables it is obvious that a very considerable portion of the inbreeding shown in the pedigree of King Melia Rioter 14th arises from the fact that his sire and dam were closely related. Furthermore, both sire and dam are closely inbred in their own lines. The curve of total inbreeding in this case is shown in Fig. 1, along with the curves for continued brother × sister, parent by offspring, and cousin × cousin mating.

TABLE IV

SUMMARIZED PEDIGREE ELIMINATION TABLE FOR KING MELIA RIOTER 14TH

Generation	2	3	4	5	6	7	8	9	10	11	12
♂ only			1	3	16	41	105	219	447	898	1,796
♀ only				1	2	4	8	16	32	64	128
Cross-over	1	2	5	12	28	59	119	240	480	960	1,920
Together	1	2	6	16	46	104	232	475	959	1,922	3,844

From this we have, for the inbreeding coefficients,

$$
\begin{aligned}
Z_0 &= 0\\
Z_1 &= 25.00\\
Z_2 &= 25.00\\
Z_3 &= 37.50\\
Z_4 &= 50.00\\
Z_5 &= 71.88\\
Z_6 &= 81.25\\
Z_7 &= 90.63\\
Z_8 &= 92.77\\
Z_9 &= 93.65\\
Z_{10} &= 93.85\\
Z_{11} &= 93.85
\end{aligned}
$$

These facts will possibly be made clearer to those not actually working much with pedigrees by Table V, which gives the first four ancestral generations[4] of the pedigree of King Melia Rioter 14th.

Generalizing the above reasoning we get the following result.

In A_3, and higher ancestral generations, $2/4 = 50.00$ per cent. of the dam's ancestors are animals which are also ancestors of the sire.

In A_4, and higher ancestral generations, $5/8 = 62.50$ per cent. of the dam's ancestors are animals which are also ancestors of the sire.

In A_5, and higher ancestral generations, $12/16 = 75.00$ per cent. of the dam's ancestors are animals which are also ancestors of the sire.

In A_6, and higher ancestral generations, $28/32 = 87.50$ per cent. of the dam's ancestors are animals which are also ancestors of the sire.

In A_7, and higher ancestral generations, $59/64 = 92.19$ per cent. of the dam's ancestors are animals which are also ancestors of the sire.

[4] In the study of pedigrees stress is naturally laid on the ancestral generations, rather than on the filial, as in breeding experiments. It becomes very convenient to have a brief designation for ancestral generations, in the same way that F_1, F_2, etc., are used to denote filial generations. I would suggest the use of the letter A with sub-numbers for this purpose. We then have A_1 denoting the parental generation, A_2 the grandparental, A_3 the great-parental, etc.

In A_8, and higher ancestral generations, $119/128 = 92.97$ per cent. of the dam's ancestors are animals which are also ancestors of the sire.

In A_9, and higher ancestral generations, $240/256 = 93.75$ per cent. of the dam's ancestors are animals which are also ancestors of the sire.

In A_{10}, and higher ancestral generations, 93.75 per cent. of the dam's ancestors are animals which are also ancestors of the sire.

In A_{11}, and higher ancestral generations, 93.75 per cent. of the dam's ancestors are animals which are also ancestors of the sire.

In A_{12}, and higher ancestral generations. 93.75 per cent. of the dam's ancestors are animals which are also ancestors of the sire.

TABLE V

Pedigree for Four Ancestral Generations of King Melia Rioter 14th

Sex ♂				
No. 103901 King Melia Rioter 14th.	♂ No. 73104 King Melia Rioter.	No. 63200 ♂ Marjorie Melia Ann's Son.	No. 56581 ♂ Melia Ann's King.	No. 22041 ♂ Melia Ann's Son.
				No. 100775 ♀ Lottie Melia Ann.
			No. 157263 ♀ Marjorie Melia Ann.	No. 22041 ♂ ● Melia Ann's Son.
				No. 905883 ♀ Mary Melia Ann.
		No. 181544 ♀ Letty Silver Hair.	No. 58169 ♂ King of All Kings.	No. 54896 ♂ St. Lambert's Rioter King.
				No. 114804 ♀ St. Lambert's Letty.
			No. 148456 ♀ Exile's Silver Hair.	No. 32559 ♂ Exile of St. Anne's.
				No. 60449 ♀ Silver Hair 4th.
	♀ No. 262926 Larissa Marie.	No. 73104 ♂ ● King Melia Rioter.	No. 63200 ♂ ⊗ Marjorie Melia Ann's Son.	No. 56581 ♂ ⊗ Melia Ann's King.
				No. 157263 ♀ ⊗ Marjorie Melia Ann.
			No. 181544 ♀ ⊗ Letty Silver Hair.	No. 58169 ♂ ⊗ King of All Kings.
				No. 148456 ♀ ⊗ Exile's Silver Hair.
		No. 219360 ♀ Dula Riotress Maid.	No. 62098 ♂ King Rioter's Lad.	No. 54896 ♂ ● St. Lambert's Rioter King.
				No. 142296 ♀ King's Riotress Nora.
			No. 218796 ♀ St. Lambert's Dula Riotress.	No. 57778 ♂ St. Lambert's Boy.
				No. 174761 ♀ Rioter Lad's First Daughter.

These percentages are quantities of a good deal of interest. They measure the degree in which King Melia Rioter 14th's sire and dam were related to each other. Community of ancestry is the basis of kinship.

Percentages derived in the way shown above, from cross pedigree elimination tables, I propose to call *coefficients* of relationship, and to designate by the letter K, with appropriate sub-numbers referring to the generation. These relationship coefficients are, with some limitations, independent of the inbreeding coefficients in the values they may take, though the two will usually be correlated to some degree. It is, however, possible to have a high value of Z with $K=0$.

TABLE VI

Comparing the Maximum Possible Values of the Coefficients of Inbreeding (Z) when the Coefficient of Relationship K Equals (a) Zero, and (b) 100

Generation	Maximum Possible Value of Z when $K=0$	Maximum Possible Value of Z when $K=100$
A_1	0	0
A_2	0	50.00
A_3	50.00	75.00
A_4	75.00	87.50
A_5	87.50	93.75
A_6	93.75	96.88
A_7	96.88	98.44
A_8	98.44	99.22
A_9	99.22	99.61
A_{10}	99.61	99.80

The most important feature of the relationship coefficients is found in their genetic implications. This can be indicated best by an illustration. Let us consider the case of the maximum possible degree of inbreeding with $K=0$. This will be found when the sire and the dam are each inbred to the highest possible degree (continued brother $\times$ sister mating) but are in no way related to each other. Such a case would be afforded, for example, if a Jersey bull, the product of continued brother $\times$ sister mating, was bred to a Holstein cow, which was also the product

of a continued brother by sister breeding. Clearly K would be 0, since no animal on one half of the pedigree could even appear on the other. The values of the successive coefficients of inbreeding (Z's) in such a case are shown in Table VI, where they are compared with the coefficients of inbreeding in complete continued brother × sister mating, where $K = 100$.[5]

From this it appears that an individual may be inbred in 10 generations to within two tenths of one per cent. as intensely, measured by the coefficients of inbreeding, if his sire and dam are in no way related, as he would be if his sire and dam were brother and sister. But clearly the germinal constitution of the individual produced would, except by the most remote chance, be quite different in the two cases. This point is so evident as to need no elaboration. It has been brought out by East and Hayes.[6]

The values of the K's for a particular pedigree evidently furnish a rough index of the probability that the two germ-plasms which unite to form an individual are alike in their constitution. This will follow because of the fact that the probability of likeness of germinal constitution in two individuals must tend to increase as the number of ancestors common to the two increases. Just what is the law of this increase in probability is a problem in Mendelian mathematics which has not yet been worked out. The general fact, however, seems quite sure.

From the above discussion it seems plain that in reaching a numerical measure of the degree of inbreeding it is not sufficient to consider coefficients of inbreeding alone. The coefficients of relationship must also be taken into account.

It is suggested that the two constants be written together for each generation, the coefficient of inbreeding being followed by the coefficient of relationship in brackets. Thus we have

[5] Since, of course, *all* of a sister's ancestors are identical with her brother's.

[6] U. S. Dept. Agr. Bur. Plant Industry, Bul. No. 243, pp. 1–58, 1912.

INBREEDING AND RELATIONSHIP COEFFICIENTS OF KING MELIA RIOTER 14TH

$Z_0(K_1) = 0$	(0)
$Z_1(K_2) = 25$	(0)
$Z_2(K_3) = 25.00$	(50.00)
$Z_3(K_4) = 37.50$	(62.50)
$Z_4(K_5) = 50.00$	(75.00)
$Z_5(K_6) = 71.88$	(87.50)
$Z_6(K_7) = 81.25$	(92.19)
$Z_7(K_8) = 90.63$	(92.97)
$Z_8(K_9) = 92.77$	(93.75)
$Z_9(K_{10}) = 93.65$	(93.75)
$Z_{10}(K_{11}) = 93.85$	(93.75)
$Z_{11}(K_{12}) = 93.85$	(93.75)

The physical meaning of these expressions is simple and straightforward. $Z_4(K_5)$ tells us that in the 5th ancestral generation of King Melia Rioter 14th he had only one half as many different ancestors as was possible for that generation, and of his ancestors three fourths were common to his sire and his dam. However one looks at the matter there can be no denial that King Melia Rioter 14th is a closely inbred animal.

In Fig. 1 the heavy broken line gives the relationship coefficients for King Melia Rioter 14th. It will be instructive now to consider another example by way of contrast. Again a Jersey bull, Blossom's Glorene (102701), will be taken. Only the final result need be given.

INBREEDING AND RELATIONSHIP COEFFICIENTS OF BLOSSOM'S GLORENE

$Z_0(K_1) = 0$	(0)
$Z_1(K_2) = 0$	(0)
$Z_2(K_3) = 12.50$	(0)
$Z_3(K_4) = 12.50$	(0)
$Z_4(K_5) = 25.00$	(0)
$Z_5(K_6) = 29.69$	(0)
$Z_6(K_7) = 35.94$	(0)
$Z_7(K_8) = 40.23$	(0)

The total inbreeding and the relationship curves are given in Fig. 2.

The difference in the breeding of this bull and the one considered in the former example is striking. In the 8th ancestral generation Blossom's Glorene has but 60 per

cent. of the number of different ancestors possible in that generation, but not one single animal in the ancestry of his sire occurs in the ancestry of his dam (within the limits A_1 to A_8). The probability is that Blossom's Glorene is heterozygous in respect of most of his characters, while King Melia Rioter 14th is homozygous.

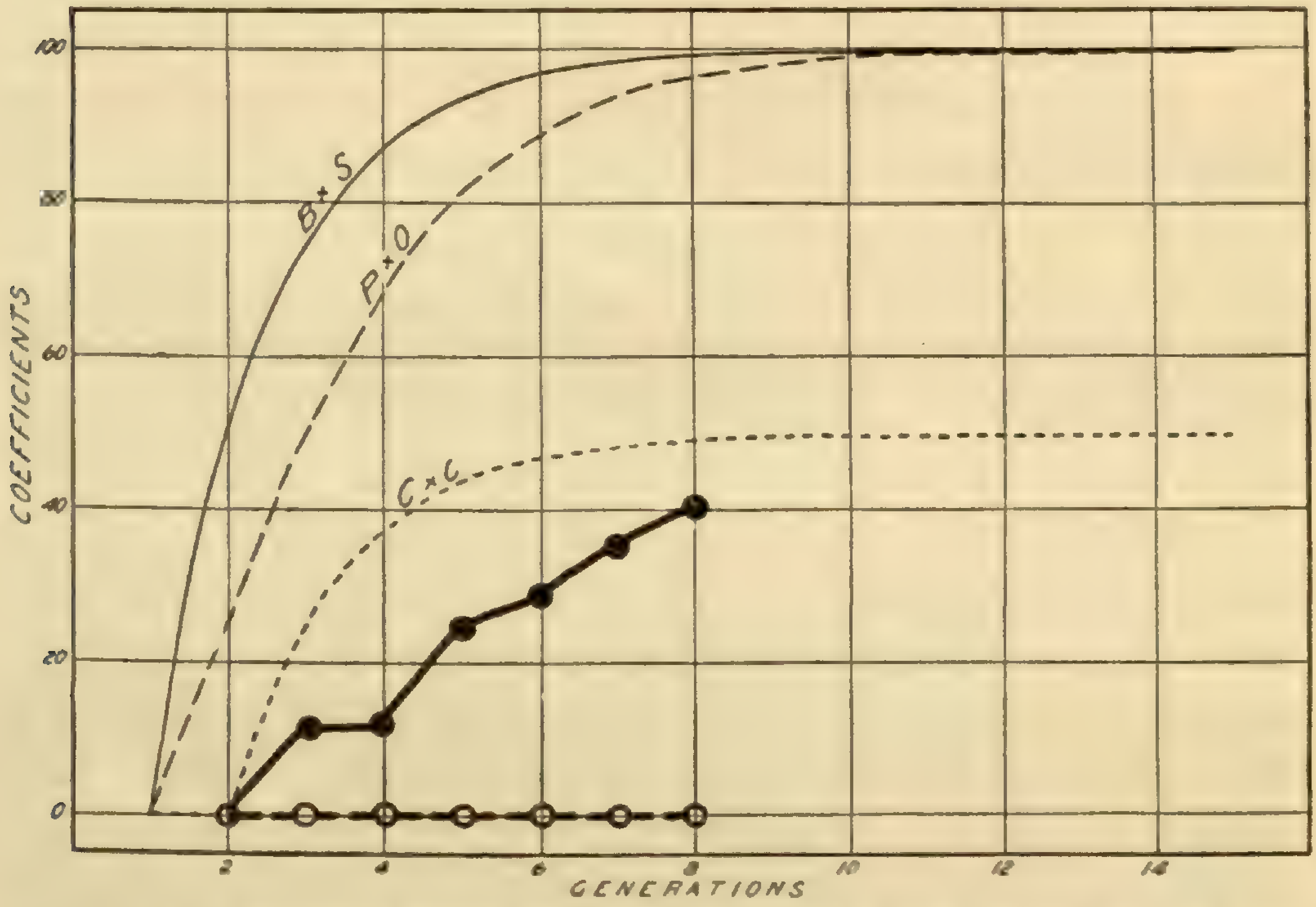

FIG. 2. Diagram showing the total inbreeding (heavy solid line) and the relationship (heavy broken line) curves for the Jersey bull Blossom's Glorene, over a period of eight ancestral generations. Compare with Fig. 1.

SUMMARY

The object of this paper is to call attention to the fact that inbreeding of considerable degree may exist in the entire absence of any kinship between the two individuals bred together, and to bring forward a method of separately measuring what proportion of the observed inbreeding in a particular case is due to kinship of the parents, and what to earlier ancestral reduplication. A proposed coefficient of relationship is described, and its application illustrated by concrete cases.

THE CHROMOSOME HYPOTHESIS OF LINKAGE APPLIED TO CASES IN SWEET PEAS AND PRIMULA

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There are two views as to the nature of linkage. The earlier view, developed by Bateson and his co-workers, is that this phenomenon is an expression of symmetrical reduplications in the germ tract. A more recent view, developed by Morgan and his co-workers, treats linkage on the basis of a linear arrangement of genes in the chromosomes and of the history of these genes during normal gametogenesis. The advocates of the reduplication view have rarely applied their principles to the results on *Drosophila* on the ground that the results for *Drosophila* are complicated by sex-linkage. That sex-linkage is simply an additional, but wholly independent, phenomenon, is proven by the many cases in *Drosophila* in which sex-linkage is not involved, yet in which the linkage of the genes to each other is of the same type as the linkage of sex-linked genes to each other.

In this paper I shall attempt to show that the theory of linkage which we have successfully applied to all cases in *Drosophila*, whether involving sex-linked genes or genes which show no sex-linkage, applies equally well to the non-sex-linked cases occurring in sweet peas and primula. The only serious drawback to such an application lies in the nature of the data which have been collected for these cases. The least satisfactory form of data from which to determine a linkage value is that presented by F_2 results. In cases in which two recessives enter from opposite parents ("repulsion"), the excessive smallness of the double recessive class in F_2 renders any calculation subject to great error. Slightly better are the F_2 results from coupling,

but here there is no direct parallelism between the zygotic and gametic ratios. In determining what gametic ratio underlies the F_2 results given by an experiment, the practise has been to compare by the eye the given result with a series of F_2 results calculated from selected gametic ratios. Collins has shown[1] that this practise has led to serious error. In F_2 coupling cases in which there has been no crossing over in one sex (autosome genes in *Drosophila*), there is a *direct* relation between the gametic and zygotic series, but only in certain classes which comprise from one fourth to less than one half of the individuals of an experiment. While such data are more accurate than the usual F_2 results, yet the percentage of individuals which can be used directly is so low that we avoid the use of such a method. In F_2 results involving only sex-linked genes, the efficiency is at least 50 per cent., for here there is always a direct relation between the gametic and zygotic ratios in one half the flies (the males). However, half the total number of flies (the females) are useless unless the cross is made in such a way that F_2 becomes a back cross. These different kinds of F_2 results (the two most advantageous of which are not generally applicable) are separated in effectiveness by a wide gap from the back cross which we use equally well in all cases, which gives a zygotic ratio directly proportional to the gametic ratio, and in which *every* individual occurs in the most advantageous relations.

Perhaps the least unsatisfactory method of dealing with such F_2 series as are available in the case of the sweet peas, is by means of the coefficient of association as derived by Yule. Yule's coefficient of association is calculated from a zygotic series of the form $AB:aB:Ab:ab$ by the formula:

$$\text{Coefficient of association} = \frac{(AB \times ab) - (aB \times Ab)}{(AB \times ab) + (aB \times Ab)}.$$

To find the gametic ratio corresponding to this coefficient, use is made of a table which gives the coefficients

[1] Am. Nat., '12.

calculated from the zygotic series corresponding to such gametic ratios as 2.5:1, 3:1, 3.5:1, etc. For the same ratio in the coupling and repulsion series the coefficients are slightly different, so that two tables should be made.

Upon the chromosome basis the best method of expressing the amount of linkage is in terms of percentage of crossing over. The gametic ratio $n:1$ found through the coefficient of association, when expressed as a percentage becomes $\frac{100}{n+1}$.

According to the chromosome hypothesis, all genes which are linked to each other lie in the same chromosome. In sweet peas the first case in which linkage was observed was that of round pollen[2] and red flower color. Later it was found that hooded standard was linked to round and to red. The genes for these three characters, then, may be treated as though carried by the same chromosome, which we may call chromosome I, of the sweet pea.

The relative distances of these genes from one another in the chromosome can be determined from the degrees of linkage. The farther apart in the chromosome any two genes lie, the greater will be the amount of crossing over between them. If two genes lie very close together, then the percentage of crossing-over will be very small (the gametic ratio very large).

Fortunately Punnett has recently collected the data upon these linkage cases in sweet peas. In the table which follows, I have summarized the data given by the various tables of Punnett. In the first column to the right of the data appear the coefficients of association. In the next column appear the corresponding gametic ratios calculated by interpolation to the nearest tenth. In the last column are the equivalent percentages of crossing over, found from the gametic ratios.

We may use one per cent. of crossing over as our unit of distance in measuring the space between two genes.

[2] I have used a terminology here like that used for the cases in *Drosophila*, naming the gene after that member of the pair of allelomorphs which may be considered as the mutant from the wild type of pea.

The gene for red is then about eleven units from that for round, and the gene for hooded is nearly one unit from that for red.

TABLE I

CHROMOSOME I

	Wild Type				Coefficient of Association	Gametic Ratio	Percentage of Cross-overs
Round Pollen and Red Color							
	Wild Type	Round	Red	Round Red			
Coupling	...7,897	583	614	2,197	.9596	7.9:1	11.2
Red Color and Hooded Standard							
	Wild Type	Red	Hooded	Red Hooded			
Coupling	...2,568	16	17	857	.9998	125.:1	.8
Round Pollen and Hooded Standard							
	Wild Type	Round	Hooded	Round Hooded			
Coupling	... 626	74	83	174	.8932	4.7:1	18.
Repulsion	...3,140	1,413	1,438	14	.9577	8.7:1	10.3

The order of arrangement of these genes in the chromosome can be discovered from a comparison of the linkage values found above. The linkage value (11.2) for round and red is the most accurately determined of those involved, so that we may lay this down as our initial or base line:

DIAGRAM I. R_0 = round pollen, R = red flower.

The next most accurate value is that for red and hooded, namely, 0.8. Hooded lies therefore only about one unit from red, but if these two values only, namely, round red and red hooded, were given, we should be unable to decide whether hooded lies between round and red at a position near 10 (that is, 11.2 — .8) or beyond red in a locus at 12 (that is, 11.2 + .8). In order to determine whether hooded lies to the left or to the right of red the data for the third value, round hooded, need only be accurate enough for us to decide between these values of 10

and of 12 units. The data from the coupling experiments (which even though less extensive then those from the repulsion experiments are probably more accurate) give a value of about 18 units. Since the repulsion data give 10 units, 18 is probably too high, and an intermediate position correct. The higher (12) of the two possible values is then the correct value. The position at 10 is not excluded by these data, but is far less probable. In a case in which one of the two first values is very small, as here, the accuracy demanded of the remaining or third value is much greater than in cases where neither of the values are small, and one has only to decide between two very different values by aid of the third. There are other ways of arriving at this order of genes which are independent of the size of the values. One of those methods, such for example, as that of double crossing over, would definitely settle the order of these three genes, but unfortunately such data have not yet been published.

If hooded lies beyond red at 12, the complete first chromosome diagram will be as follows:

DIAGRAM II. Chromosome I, Sweet Pea. R_0 = round pollen, R = red flower, H = hooded.

In the above diagram R_0 indicates the locus of round (and also of long). The symbols in the diagrams are used to designate loci which may be occupied by either allelomorph of the pair.

It has been observed that hooded flowers have always a uniform color in standard and wings, instead of having these two regions colored differently as in the normal or bicolor type. Bateson assumed that this unicolorism was only another somatic effect of the hooded gene. However, an alternative explanation is that the unicolor is caused by a specific gene which is very closely linked to hooded. If this should be found to be the case, then this fourth gene also will be located at about 12 units from round.

There is one other gene which probably belongs in the first chromosome, namely, the intensifier found in the "black knight" race. The linkage data of red color and intensity of color have been given in Report II to the Evolution Committee, page 90.

TABLE II

Red Color and Intense Color

	Wild Type	Red	Intense	Red Intense	Coefficient of Association	Gametic Ratio	Percentage of Cross-overs
Coupling ...	149	29	35	22	.527	1.9:1	35.

If these data are significant, then intense is in the first chromosome at a locus about 35 to the right or left of red. It should give about 24 (35 − 11) or 46 (35 + 11) per cent. of crossing over with round, depending on whether it lies about 24 to the left of round or 35 to the right of red.

The Second Chromosome of Sweet Peas

In the case of the second chromosome in sweet peas, the linkage values are based on smaller numbers, but the order of genes is more certain.

The first linkage case of this chromosome was that of sterile anthers and light axils. Later the cretin form of flower was found to belong to this linkage group. As in the case of the first chromosome, I have summarized the tables of Punnett in Table III.

TABLE III

Chromosome II

Sterile Anthers and Light Axil

	Wild Type	Sterile	Light	Sterile Light	Coefficient of Association	Gametic Ratio	Percentage of Cross-overs
Coupling ...	1,170	41	30	379	.9945	22.:1	4.4
Repulsion ..	1,335	643	714	2	.988	20.:1	4.9

Light Axils and Cretin Flower

	Wild Type	Light	Cretin	Light Cretin			
Coupling ...	282	49	52	59	.734	2.6:1	28.
Repulsion ..	48	22	27	3	.610	2.7:1	27.

Sterile Anthers and Cretin Flower

	Wild Type	Sterile	Cretin	Sterile Cretin			
Coupling ...	165	58	58	78	.556	2.:1	33.
Repulsion ..	764	355	345	25	.683	2.6:1	28.

The linkage value for sterile and light, namely, 4.4 units, is the most accurately determined of those in the second chromosome. The value for light and cretin is about 28 units. Using the distance 4.4 between sterile and light as our base line, then, we should find that cretin lies at $4 + 28$ or 32 from sterile if the order of genes is sterile, light, cretin; but if the order is cretin, sterile, light, then cretin should lie at $28 - 4$ or 24 from sterile. The value for sterile cretin should approximate either 24 or 32. There is no very small value here as there was in the first chromosome, and not such great accuracy is required of the remaining value, since it should be easy to distinguish between 24 and 32. The coupling data for this value gives 33 units, which enables us to fix the order of genes as sterile, light, cretin. The following diagram of chromosome II expresses these relations more clearly.

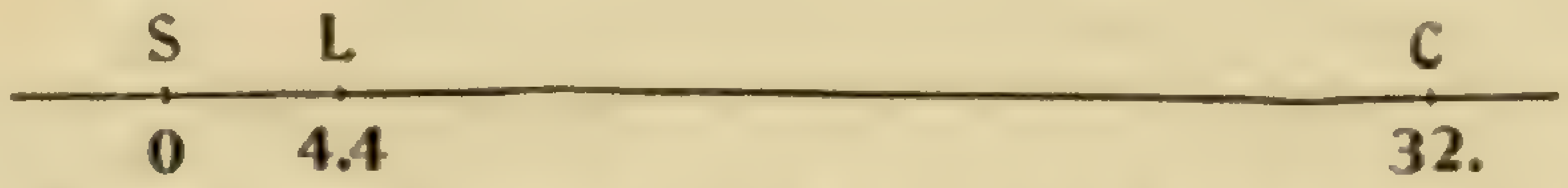

DIAGRAM III. Chromosome II, Sweat Pea. S = sterile, L = light, C = cretin.

When crossing over is as free as in the case of sterile and cretin and of light and cretin there should be some double crossing over. That is, crossing over might occur in the section of the chromosome near sterile and light and at the same time another crossover could occur in the section between light and cretin. This occurrence would be readily seen if normal plants heterozygous in any combination of these three genes were back-crossed to plants purely recessive in all three. A relatively few plants from such a test would give very valuable information on several points, while an experiment of a few thousand individuals from such back-cross tests would enable one to discover, through the phenomenon of interference, much

as to the character of the chromosome, the average length of the internode, and the percentage of chiasmas per node.

Independence of Chromosomes I and II of Sweet Peas

If two groups of genes are carried by separate chromosomes, we may expect to obtain free assortment and typical 9:3:3:1 ratios in F_2, when any two genes from different groups are involved. There are rather extensive data for three such cases in sweet peas, and in each there is practically complete independence. The data given in Table IV are summarized from Report III to the Evolution Committee (page 37) and Report IV (page 17).

TABLE IV

Independence of the First and Second Chromosomes

Round Pollen (1st) and Light Axil (2d)

Wild Type	Round	Light	Round Light	Coefficient of Association	Gametic Ratio	Percentage of Cross-overs
1,246	341	399	142	.131	1.15:1	47.

Red Color (1st) and Light Axil (2d)

Wild Type	Red	Light	Red Light			
1,563	545	506	232	.136	1.16:1	47.

Red Color (1st) and Sterile Anthers (2d)

Wild Type	Red	Sterile	Red Sterile			
838	403	265	147	.071	1.07:1	48.

The greatest departure from the 50 per cent. of crossing over expected from independent assortment is only to 47 per cent.

There are several other characters whose genes seem to be independent of those in the first and second chromosomes. This is interesting from the point of view that each independent gene or group of linked genes requires a distinct chromosome as a carrier.

LINKAGE CASES IN PRIMULA

In the case of primula, linkage was first found between red (versus green) stigma and red (versus magenta) flower color. Long style (versus short) and dark stem (versus light) were found to be linked with red stigma. Indications were observed that still a fifth gene, a dominant which reduces the color of the flower to a tinge in the corolla tube, belonged to this group.

A back cross involving the three genes, red stigma, red flower and long style was made. Credit is due to Gregory for the use of this method for obtaining linkage data. Unfortunately many of the individuals were useless for the linkage of red flower color, because of the occurrence of white; and the numbers are small.

In Table V, I have summarized the data given by Gregory.[4]

TABLE V

THE FIRST CHROMOSOME OF PRIMULA

Red Stigma and Red Flower

	Non-crossovers		Crossovers				
	Red Stigma Red Flower	Wild Type	Red Stigma	Red Flower	Coefficient of Association	Gametic Ratio	Percentage of Cross-overs
Coupling back cross	28	39	17	18		1.9:1	34.6
	Wild Type	Red Stigma	Red Flower	Red Stigma Red Flower			
Coupling F_2	1,174	305	289	232	.511	1.8:1	35.3

Red Flower and Long Style

	Non-crossovers		Crossovers				
	Red Long	Wild Type	Red	Long			
Coupling back cross	40	53	6	5		8.4:1	10.9
	Wild Type	Red	Long	Red Long			
Coupling F_2	38	2	4	12	.966	8.6:1	10.4

Red Stigma and Long Style

	Non-crossovers		Crossovers				
	Red Stigma Long	Wild Type	Red Stigma	Long			
Coupling back cross	44	64	35	30		1.6:1	37.

[4] *Jour. Genetics,* '11, Vol. I; *Proc. Roy. Soc.,* '11, Vol. —, 84.

Red Stigma and Dark Stem

	Wild Type	Red Stigma	Dark	Red Stigma Dark			
Repulsion	137	66	62	0	—	—	—

The three values are—red stigma red flower 35, red flower long style 11, and red stigma long style 37. Of these, red stigma red flower is based upon the most data, and may therefore be taken as our base line. The value for red stigma long style should be 35 — 11 or 24, if the order of genes is long, red stigma, red flower; but 35 + 11 or 46, if the order of genes is red stigma, red flower, long. The value shown by the table is 37. This means that long lies to the right of red at a locus 46.

DIAGRAM IV. Chromosome I, Primula. Rs = red stigma, R = red flower, L = long style.

58 59 60 61 62

The apparent discrepancy between the values 46 and 37 is due in most part to double crossing over, the effect of which is always to lower large values disproportionately more than short. When the discrepancy is known, the amount of double crossing over can be calculated approximately. Here the amount of double crossing over is

$$\frac{46-37}{2}=4.5.$$

That is, 4.5 per cent. of all the gametes are the result of double crossing over. A somewhat larger amount of data from a back cross in which all the individuals are effective would give by direct experiment a true value for the amount of double crossing over.

A chromosome diagram should be built up of values independent of double crossing over. According to our experience with *Drosophila*, if there is not more than ten per cent. of crossing over between two genes, the double crossing over is negligible. Thus in the first chromosome in sweet peas, the values obtained from the experiments are not changed by double crossing over. However, in the

case of the second chromosome, where the total percentage of crossing over is about 32, there is probably one or two per cent. of double crossing over. The diagram of the second chromosome is in this respect only tentative, and the plotted position of cretin will be moved a little farther to the right when the amount of double crossing over between light and cretin has been found. The value 4.4 for sterile anther light axil is not affected by double crossing over, since the section of chromosome between these two loci is so short that a double break would probably not occur between them at all. The amount of double crossing over between any two loci can only be found when there is a gene between them. Thus if a gene should be found which lies between light and cretin, either by indirect calculation or, better, by direct experiment, the amount of double crossing over could be found. The more genes which can be worked with in the same chromosome, the more accurate becomes the diagram.

All the values found for these cases in sweet peas and primula are based upon such small numbers that they can be used only as illustrations of the way in which one would apply to new cases certain principles worked out in *Drosophila*. While they serve as examples in line with these principles, they are entirely inadequate as proof. A very interesting case of variation in linkage is presented by some of the families involving chromosome II of the sweet pea. In this article I have avoided such data as far as I could, but it is possible that the order in which I have aligned these genes will be found to be incorrect when data upon all three genes in a back cross are obtained. Such data would show, through the phenomenon of double crossing over, what the order of genes is, even though variations in the linkage should occur.

Columbia University,
May, 1914

THE REDUPLICATION HYPOTHESIS AS APPLIED TO DROSOPHILA

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A NUMBER of papers developing the reduplication hypothesis of linkage have recently appeared in the *Journal of Genetics*. They are based almost entirely on the experiments of Gregory ('11) on *Primula* and of Punnett ('13) on the sweet pea. The data are not entirely satisfactory because of the relatively small number of genes involved, and because in most cases the gametic ratios can be only approximately determined. This is due to the fact that most of the data concern F_2 counts, from which gametic ratios can not be calculated directly. In Gregory's best case a much more satisfactory method was followed—the heterozygous plants were tested, not by mating to others of their kind, but by crossing with plants recessive with respect to all the genes involved, which gives the gametic ratio directly. In this case, however, we have only a relatively small series of data involving as many as three pairs of linked genes. It is obvious that from such data no adequate test of the reduplication hypothesis can be made.

The phenomena of linkage have been very extensively studied. by Morgan and others, in the fly *Drosophila*. In this animal there are many genes belonging to the same linkage groups, and these have been studied on a large scale. In the case of the sex-linked group there is never any difficulty in calculating the gametic ratio from F_2 results, since the F_2 males from any cross always give it directly. I have recently published a paper (Sturtevant, '14) giving a complete summary of the published results obtained from studies of the linkage of these genes. In that paper I have adopted the chromosome explanation of link-

age proposed by Morgan ('11). Here I shall use the same data for a test of the reduplication theory. It may be of value to contrast the two views by making a rigorous application of them to the same facts. Since the data concerning the sex-linked group of genes in *Drosophila* form the simplest and most extensive series now available, I shall deal more especially with them. The reader is referred to my other paper for the detailed data, for references to original sources, and for a full treatment of the chromosome hypothesis as applied to these and other data.

It may be well to give first a brief catalogue of the sex-linked genes discussed in this paper. The nomenclature is that suggested by Morgan ('13). This may be confusing to those accustomed to the "presence and absence" system, but this should not be a serious objection here, since a clear conception of the somatic appearance of the animals discussed is not essential for our present purpose. The relations would be as clear if hieroglyphics were used for symbols.

Y is the gene which differentiates the wild "gray" bodied fly from the yellow mutant, *y*.

V differentiates the wild red-eyed fly from the vermilion-eyed mutant, *v*.

M differentiates the "long" wing of the wild fly from that of the miniature-winged mutant, *m*.

R is another gene affecting the wings. The wild fly has *R*, the rudimentary-winged mutant has *r*.

Br′ occurs in a dominant mutant form having a narrow eye known as barred. The allelomorph present in the wild fly is designated *br′*.

The other characters concerned bear such a relation to one another that the genes involved are considered as forming a system of quadruple allelomorphs. The alternative to this view is the assumption of complete linkage, but I have given elsewhere (Sturtevant, '13) my reasons for preferring the multiple allelomorph interpretation. The eye of the wild *Drosophila* is red in color. A single

mutant obtained from it had white eyes (Morgan, '10), and this character proved to be a simple sex-linked recessive. From the white-eyed form arose a fly with eosin eyes (Morgan, '12). This new character was found to be a sex-linked dominant to white, and a sex-linked recessive to red. Finally, there arose a form with cherry eye color (Safir, '13). This has the same relation to red and to white as has eosin. Mated to eosin it gives an intermediate color, which splits up into cherry, intermediate, and eosin in F_2. The nomenclature adopted in this case is as follows:

> Allelomorph present in the red-eyed fly, W.
> Allelomorph present in the white-eyed fly, w.
> Allelomorph present in the eosin-eyed fly, w^e.
> Allelomorph present in the cherry-eyed fly, w^c.

Trow ('13) has suggested the possibility of an asymmetrical reduplication series, giving a gametic series of $wAB:xAb:yaB:zab$, where w need not equal z, nor x equal y. It should be noted that an actual demonstration of such a ratio, or of its non-existence, is almost excluded for the reason that it would be practically impossible to be sure one was not dealing with a case involving differential viability. However, perhaps the most striking general fact brought out by the study of linkage is that each pair of linked genes (allelomorphs), considered separately, follows a perfectly regular Mendelian course. I think we are, therefore, justified in assuming that the number of gametes bearing A is always equal to the number bearing a, and similarly for B and b. Then, in Trow's asymmetrical series,

$$w + x = y + z,$$
$$w + y = x + z.$$

Hence,

$$w = z \quad \text{and} \quad x = y.$$

In all that follows I shall assume that the reduplication series are always symmetrical. On this assumption it becomes unnecessary to consider the two halves of the

series separately, and I shall therefore use only two terms in speaking of gametic ratios. By adding together the two halves of the series larger numbers are obtained, so that chance deviations are relatively smaller. Differential viability is also partially overcome in this way. Of course on the reduplication theory both terms of the gametic ratio must be integers, since they represent numbers of cells, but nevertheless it has seemed to me more convenient for purposes of calculation to express them always in the form $n:1$. Thus a gametic ration of 3:2 may be written 1.5:1.

It was suggested by Bateson and Punnett ('11) that the intensity of coupling and of repulsion between the same two pairs of genes may be identical. That this is substantially the case has been shown again and again in *Drosophila,* and has become a truism among those working on that form. Before presenting data on this point I wish to bring up another matter on which the same data have a bearing. Punnett ('13) has said, "But where three [pairs of] factors are concerned . . . the value of the primary reduplications is evidently altered, and there would seem to be some process whereby these reduplications react on one another." Bailey ('14) has suggested that the nature of this interaction may be such as to cause the two primary series to be of equal intensity. It may be categorically stated that *there is no interaction effect in Drosophila.* The best data for a test of the relative intensity of coupling and repulsion, and of "fundamental," "primary" and "secondary" reduplication series, involving the same allelomorphic groups, is that furnished by the relations of the various forms of W (W, w, w^e, w^c) to the M pair of allelomorphs (M and m). Table I is a summary of the data on this case. In computing the fundamental series I have used only the data from such of my own experiments as involve only two pairs of genes, since that from other sources is for the most part made up of primary series in which the other primary series involved is masked.

TABLE I

FUNDAMENTAL SERIES

Nature of Cross	Actual Numbers	Gametic Ratios
WM × *wm*	777 : 470	1.6 + : 1
Wm × *wM*	93 : 221	1 : 2.4 —
WM × *w^e^m*	634 : 348	1.8 + : 1
Wm × *w^e^M*	46 : 110	1 : 2.4 —
Wm × *w^e^M*	461 : 855	1 : 1.9 —
w^e^M × *wm*	4,171 : 1,858	2.2 + : 1
w^e^m × *wM*	891 : 1,898	1 : 2.1 +
w^e^M × *wm*	75 : 47	1.6 : 1

PRIMARY SERIES

Nature of Cross	Actual Numbers	Gametic Ratio	Other Primary Series Involved
WM × *w^e^m*	178 : 85	2.1 — : 1	*MBr'*
w^e^m × *wM*	69 : 122	1 : 1.8 —	*MBr'*
WM × *wm*	5,838 : 2,911	2.0 + : 1	*YW*
Wm × *wM*	1,111 : 2,493	1 : 2.2 +	*YW*
WM × *wm*	2,261 : 1,011	2.2 + : 1	*MR*
	Secondary Series		Primary Series
WM × *w^e^m*	719 : 407	1.8 — : 1	*WV, VM*
Wm × *w^e^M*	227 : 509	1 : 2.2 —	WV, VM

It will be noted that in all these cases the gametic ratio approximates 2 : 1, or 1 : 2, according to the nature of the cross. There are only four cases showing a noticeable deviation from this value, and of these two involve only small counts. The most serious is the first. In this case there is a deviation of 54.3 from the 2 : 1 ratio, and the standard error is 16.7[$\sqrt{1/3 \times 2/3 \times (777 + 470)} = \pm 16.7-$]. Since the deviation is slightly over three times the standard error, it is perhaps significant, especially since there is at least one other rather large deviation (the second ratio in Table I). For our present purpose, however, it is probably not significant, since similar deviations occur in different experiments of exactly the same type. I have recorded elsewhere (Sturtevant, '14) the results of a number of tests of individual females heterozygous for these two allelomorphic groups. Taking only those cultures which produced 100 or more flies, we find the following results:

Seven females of the constitution $w^e m w M$ gave gametic ratios ranging from 1.5:1 to 2.7:1, with the modal class at about 2.0:1.

Seventeen females $w^e M w m$ gave ratios ranging from 1.5:1 to 3.4:1, with a single individual at 4.2:1. The modal class was at about 2.2:1.

It seems highly probable that all these deviations from a 2:1 ratio, not due to insufficient numbers, may be satisfactorily explained on the basis of differential viability, which is known to occur here (for a discussion of the vagaries of differential viability see Bridges and Sturtevant, '14). I do not wish to be understood as arguing that the gametic ratio for any two pairs of genes is absolutely constant, but only that it is in most cases uninfluenced by the way in which the genes are combined and by heterozygosis for other genes. That it may sometimes show marked differences is now well established. I have myself studied two cases of this sort, and I have good evidence (not yet published in detail) that there are definite genes which cause great differences in the gametic ratios for whole linkage groups. In one case this gene itself shows linkage to those in the group it affects. But even here the intensity of coupling and of repulsion is affected alike, and it makes no difference how few or how many genes a fly is heterozygous for; the linkage is strong or weak according to the form of the linkage-affecting gene which the fly happens to carry. In each of these cases I have been able to obtain about the same extreme values both for coupling and for repulsion.

In what follows I shall assume that the intensity of the reduplication series is not affected by the way in which the genes are introduced, nor by the number of linked genes involved in the cross. The obvious corollary of this is that reduplication occurs even in homozygous individuals, and that the nature of the series of divisions is in general independent of the constitution of the individual. This conclusion is directly opposed to the point of view expressed more especially by Punnett, in the

passage quoted above and elsewhere. If reduplication occurs at all it is the same in the wild fly as in the most complex linkage experiment we have yet carried out.

If it is assumed that the intensity of coupling and repulsion is identical, it becomes unnecessary to consider them separately. I shall therefore lump together all the data involving the same groups of allelomorphs, regardless of how they were put into the cross. When three pairs of genes are involved there are eight possible combinations of them in F_2, but only four if we add together the two halves of the reduplication diagram. There are the two original combinations, which I shall designate *ABC*. Then there are three combinations derived from each of these by a shifting of one gene, which I shall designate *ABc*, *AbC* and *aBC*, the small letters referring to those pairs which have been shifted. Thus, to take an imaginary case, if we cross *LMn* by *lmN*, the gametes produced by the F_1 individuals will be classified as follows:

ABC	*ABc*	*AbC*	*aBC*
LMn	*LMN*	*Lmn*	*lMn*
lmN	*lmn*	*lMN*	*LmN*

In the following tables I shall reduce all data to this form. In each case the genes will be arranged so that *AB* and *BC* will be the primary reduplication series.[1]

Table II contains such a summary of all the crosses involving three pairs of sex-linked genes. Table III shows the gametic ratios derived from these data, and also the values for the secondary series calculated on the basis of Trow's "special" hypothesis. For the sake of brevity only one term is used: a gametic ratio of 3:1 is written 3; a ratio of 3:2 becomes 1.5, etc. With the simplifications introduced here Trow's formula becomes

$$AC = \frac{(AB \times BC) + 1}{AB + BC}.$$

[1] As was pointed out by Punnett ('13), in a system of three reduplication series the one with the lowest intensity is to be regarded as the secondary series.

TABLE II

Allelomorphic Groups	*ABC*	*ABc*	*AbC*	*aBC*
YWM	8,212	4,013	9	119
YWR	278	160	0	1
YVM	1,082	58	22	665
YVR	315	138	55	196
YVBr′	93	34	10	54
WVM	194	11	1	102
WMR	1,726	535	139	872
WMBr′	220	73	25	129

TABLE III

Experiment	Gametic ratios			
	Observed			Calculated
	AB	*BC*	*AC*	*AC*
YWM	95.5	2.1	2.0 –	2.0 +
YWR	438.0	1.74	1.72	1.74
YVM	1.7	22.0	1.5	1.6
YVR	1.8	2.6	1.1	1.3
YVBr′	2.0	3.4	1.3	1.4
WVM	2.0	24.7	1.7	1.9
WMR	2.2	3.9	1.3	1.6
WMBr′	1.9	3.6	1.2	1.4

It will be seen that in every case the calculated value for the secondary reduplication is higher than the observed value. The same relation comes out in two experiments which I have done involving genes of another group in *Drosophila* (see Table VIII, Sturtevant, '14). Punnett's case is so involved that calculations accurate enough for our present purpose can not be made. In Gregory's experiment one of the genes (M) could not be followed in all the plants because masked by another gene. We are not given the data for S and G in those plants in which M was classified separately from those in which it was not. The data are therefore not available for exact calculations, since the numbers are too small to overcome chance deviations. The data for my own two experiments appear in Table IV.

The same relation comes out more strikingly in another way. If we let m equal the intensity of the AB series and n that of the BC series, then on Trow's special hypothesis

the four kinds of gametes should occur in the following proportions:

$$ABC - mn$$
$$ABc - m$$
$$aBC - n$$
$$AbC - 1$$

TABLE IV

Experiment	Observed			Calculated
	AB	*BC*	*AC*	*AC*
BVgCv	3.4	11.6	2.4	2.7
BCvSp	2.5	2.1	1.0	1.4

That is, $1/(m+1)$ of the gametes should have A and B interchanged. Of these, $1/(n+1)$ should have B and C also interchanged. If N represents the total number of gametes, then the size of the AbC class should be represented by the expression

$$AbC = \frac{N}{(m+1)(n+1)}.$$

Table V shows the relation between the size of this class as observed and as thus calculated, in the ten experiments.

TABLE V

Allelomorphic Groups	*ABC* Observed	*ABC* Calculated
YWM	9	42
YWR	0	0
YVM	22	30
YVR	55	69
YVBr′	10	15
WVM	1	4
WMR	139	208
WMBr′	25	34
BVgCv	2	7
BCvSp	12	20

Thus it appears that in all ten experiments Trow's formula gives values for the AC series and for the AbC

term which are too large. Moreover, this feature appears in a more complex cross which I have carried out, involving four pairs of linked genes ($YWVM$), and in each separate part of all these experiments, regardless of how the crosses were made. It may, then, be taken as a constant relation. It can only mean that there is some relation between A and C besides that resulting from secondary reduplication. In other words, to use Bailey's terms, Trow's "special" hypothesis is not valid.

Let us then examine what Bailey calls Trow's "general" hypothesis. Suppose the primary series to be of the following values:

$$AB = l:1,$$
$$BC = m:1,$$
$$AC = n:1.$$

Trow's general formula for calculating what should be the observed value of the AC series is

$$AC = \frac{lmn + n}{l + m}.$$

The special formula is derived from this by assuming $n = 1$, when the formula becomes

$$AC = \frac{lm + 1}{l + m}.$$

Since this always gives a value which is too large, it follows that n is always less than one. This means that the AC primary series is reversed—that the combinations present in the parents tend to be reproduced in fewer numbers than the new combinations. I have worked this out for the case of $BCvSp$ (see Table IV), and find the primary series there to be 0.6:1, though the observed series is 1.0. The "fundamental" AC series has been obtained for most of the cases in Table III, and has always been found to be of the usual form (*i. e.*, $n:1$,

where $n > 1$). (See Table I, Sturtevant, '14.) In fact, as stated above, the fundamental series always approximates the secondary (observed) series.

There are two hypotheses as to the mechanics of reduplication series where more than two pairs of genes are involved. The first was suggested by Bateson and Punnett ('11), and consists in the assumption that when three pairs are involved eight cells are formed by three successive divisions, each of which segregates one pair of genes. The eight cells then represent the eight possible kinds of gametes, and are supposed to reduplicate independently until the proper proportions are reached. Bailey supposes that if it be shown that two primary series do not interact on each other this scheme will be more likely to be correct than will Trow's, which I shall discuss next. It seems to me, however, that this hypothesis begs the question. It is derived entirely by working backwards from the observed results; it affords no basis for predictions; and it does not offer a simple mechanical explanation of any of the observed results. For pragmatic reasons I believe we should adopt it only as a last resort.

Trow supposes that two cell divisions occur, segregating two pairs of genes. The four resulting cells then go through with their reduplication, which is a primary one. When this is finished there occur divisions which segregate the other pair, and the other primary reduplication is carried out. On Trow's general hypothesis, which I have tried to show is the only one which can hold, it is supposed that the second series of reduplications is affected by both of the first two pairs of genes. *C* is reduplicating more if with *B* than if with *b*, less if with *A* than if with *a*. This scheme of Trow's has one great advantage in that it accounts for the fact that the class which I have called *AbC* is always the smallest one. Reference to Trow's calculations will show that this relation should always occur, and Table II shows that it does occur. On the octant scheme there is no explanation of this relation—we simply have to assume that it does occur somehow.

It will be noted that several of the gametic ratios involved here closely approach 2:1. *YV, YM, WV* and *WM* are the most conspicuous examples. It may seem that such a simple ratio is due to a very simple reduplication series, but I do not think such an assumption can be successfully maintained. The tables given above show that *YM* and *WM* have approximately this same value when they appear as secondary series, and the data for the combination *YWVM* show the same thing for *YV* (see Sturtevant, '14).

If, as I have maintained above, the same series of reduplications must occur in all flies, whether we can follow it or not, then it follows that in these three cases the 2:1 ratio is never due to a simple series, but always to a long and complicated one, since in all three one of the primary series is of high intensity.

It was pointed out by Trow that the intensities of the reduplication series afford a method of calculating the number of cell divisions necessary to complete the series. If we assume that approximately the same series is occurring both in homozygous and in heterozygous flies, we have the following series in *Drosophila* as a basis for such calculations.

Sex-linked Group

YW = 90.1
WV = 2.1
VM = 31.8
MR = 5.0
RBr = 21.7

Second Group

BVg = 3.6
VgCv = 10.4
CvSp = 2.8
SpBa = 10 +

Third Group

PEb = 100 ±

All of these series must be considered as either primary or secondary and therefore involving primaries of higher intensity. In fact there is unpublished evidence that many of them can not be simple primaries. A number of series of very high intensity are known, and will appear in future publications. Therefore all the calculations that follow give results which are far too small.

According to Trow, the minimal number of successive cell divisions required to complete the series is given by the expression $mnp \cdots$ where m, n, p, etc., are the larger terms of the primary series involved. In the present case the value of that expression is something over 76,000,000,000. However, Trow's formula seems to be wrong. If a be the number of cell divisions required to produce m cells, then $2^a = m$. If this expression gives a value of a which is not an integer, then the next higher whole number is to be taken. In the case of the first series two divisions are necessary to segregate the genes, and in the following series one is required. The number of successive cell divisions required then is $(a+1)+(b+1)+(c+1)+\cdots+1$, where b, c, etc., bear the same relation to n, p, etc., that a does to m. In the case of *Drosophila* the value of this expression is 56. As pointed out, however, this value is certainly far too small.

The total number of cells required is given by the expression $2mnp \cdots + 2np \cdots + 2mn \cdots + 2mp \cdots + 2m \cdots + 2n \cdots + 2p \cdots + \cdots + 2mnp + 2mn + 2mp + 2np + \cdots + 2m + 2n + 2p + 1$.

This gives a value considerably above 600,000,000,000—a manifest absurdity. However, it is not necessary that all these cells should be produced, since the ratios would not be appreciably affected by some lines becoming crowded out. It is necessary, on the other hand, that all of the series shall be completed in every line which does live, since every female *Drosophila*,[2] which is of the proper constitution to be tested, shows linkage for every pair of genes tested.

[2] The results discussed here deal only with the linkage in female flies.

Thus we are forced to assume an enormously complex series of cell divisions, many of them differential, proceeding with mathematical regularity and precision, but in a manner for which direct observation furnishes no basis. It seems to me that it is not desirable to assume such a complex series of events unless we have extremely strong reasons for doing so. I can see no sound reason for adopting the reduplication hypothesis. It apparently rests on two discredited hypotheses: somatic segregation, and the occurrence of members of the 3:1, 7:1, 15:1, etc., series of gametic ratios in more cases than would be expected from a chance distribution.

The chief advantage of the chromosome hypothesis of linkage which has been proposed by Morgan ('11), and which I have followed elsewhere, seems to me to be its simplicity. In addition it appeals to a known mechanism, and a mechanism toward which the experiments of Boveri, Herbst, Baltzer and others point as the correct one. It explains everything that any of the forms of the reduplication hypothesis does, and in addition offers a simple mechanical explanation of the fact that "secondary series" are always smaller than Trow's "special hypothesis" calls for them to be. On the reduplication hypothesis this fact must merely be accepted, for, I think, it can not be explained.

Columbia University,
May, 1914

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PATTERN DEVELOPMENT IN MAMMALS AND BIRDS. III

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Partial Albinism in Wild Birds

In birds under natural conditions of wild life partial albinism is fairly common. Lists of species of which albinistic specimens are known were published by Ruthven Deane (1876, 1880) some years ago, and by others. Scattered instances are in all the bird journals or magazines of general natural history. In most cases in which the white markings are clearly defined against the pigmented parts of the plumage, these may be referred to their particular primary breaks between the several areas of pigment formation. In other cases the pigment reduction is of the diffuse type, tending to form spots.

A few instances follow in which the several primary patches have been observed in wild birds, either as accidental marks or as permanent parts of the pattern.

The Crown Patch.—In 1908, a pair of robins nested near Lowell Park, Cambridge, one of which showed a partial separation of the crown patch, through the presence of a white band, as broad as the eye's diameter, passing from one eye around the back of the head to the other eye. In the *Wilson Bulletin* (Vol. 2, p. 45, 1908) W. E. Saunders records the capture of two robins each with a white collar about the neck, probably marking the separation of the neck patches from the shoulder patches. Coues (1878) records a brood of *black* robins at St. John's, N. B., one of which was kept in captivity by the late G. A. Boardman. In September, after moulting, it was still pure black, except for white wings and tail, which seems to indicate an areal restriction of the shoulder and rump patches, though the pigment, where

produced, must have been superabundant. Ward (1908) has described a case of a black robin becoming albinistic and reviews a number of such cases. The ability of the same feather follicles in different moults to produce feathers with different sorts or amounts of pigment is thus evidenced and has lately been carefully studied by Pearl and Boring (1914) in the hen.

In addition to the case of the robin above mentioned, the white line marking off the crown patch from the ear patches is sometimes found abnormally in other birds. Thus Sweet (1907) records two slate-colored juncos (*Junco hyemalis*) taken in March, 1903, at Avon, Maine, in which there was a white line above the eye, and the black throat patch was absent, owing no doubt to the ventral restriction of the neck patches, as often seen, for example in pigeons. Maynard[1] figures the head of a young female black-poll warbler (*Dendroica striata*) in autumn, showing an inclination to assume a white superciliary stripe. I am convinced that this mark so common in many birds, is merely a development of the primary break marking off the crown patch from the ear patches so that it has become a permanent part of the pattern.

The failure of the crown patch to develop at all, as is sometimes the case in the domestic pigeon, results in a white-crowned bird. In the West Indian *Columba leucocephala,* exactly this modification has taken place and the entire top of the head is permanently white. The same condition is found in sundry other genera, including a humming bird, a heron, and others. It would be interesting to discover by experiment if it were not easier to produce a definite white marking through selecting for the non-development of a certain patch or patches, than to try to restrict a certain pigment patch to definite bounds as in the experiments of Dr. MacCurdy and Professor Castle (1907).

The crown patch as a separate unit in pigmentation, is often of a different hue from the surrounding patches.

[1] "Birds of E. North America," 1896, p. 585.

Thus in the case of the terns, the black-capped chickadee, the black-crowned night heron, and other birds, a black crown patch is noticeably marked off.

The Ear Patches.—The ear patches in birds are small, yet often specially marked out by white boundaries, which are permanent parts of the pattern. Yet there is no doubt but that the acquisition of such white boundaries is a derived character. It is common for the ear patches to be colored differently from the surrounding parts, forming as in some species of tanagers a black auricular area contrasted with the blue of the head and neck. Of particular interest in the present connection, however, are those cases in which a pigmented ear patch is more or less clearly marked off by a white line above it or below, or both. The superciliary stripe, so common in birds, is of course a development of a primary break above the patch, separating it from the crown patch. Where the stripe is narrow it is hard to say which patch has begun to be restricted, though often no doubt both are more or less involved. Thus the Garganey teal has a very wide white eye stripe, and in other species of ducks the whole side of the head may be white, indicating much greater restriction of pigment formation in contiguous patches. A beautiful example of the development of a white stripe at the *lower* border of the ear patches is found in the Inca tern, in which a line of white feathers runs from just above the gape along the lower side of the auricular patch and separates it from the dark throat. But not only is the white line developed, but the feathers composing it are specially elongated and recurved, as if the mark were one of particular decorativeness. The dark ear patch is noticeable in many hawks, separated above and below by white areas, as in the duck hawk and the osprey, though differing in the size of the white areas.

An instance in which the white line separating the crown patch from the ear patch, is even now in course of becoming established as part of the permanent pattern,

is afforded by the common guillemot (*Uria troille*) of the northern Atlantic. The other related species of the genus have the head and neck uniformly pigmented, but in *U. troille* a considerable proportion of specimens show a narrow white eyebrow and a postorbital line, in exactly the situation of the stripe in the albino robin previously noted, though not so broad nor so extended. Birds so marked were formerly considered a distinct species—the ringed murre (*Uria "ringvia"*)—or perhaps a plumage of *U. troille*, and much effort has been made to determine their exact status. Both plumages are found in the same colonies and the two sorts of birds are known to have mated together (Müller, 1862). Verrill estimated that about 40 per cent. of the nesting birds he saw on the Labrador coast were of this variety, but this is probably a rather high estimate. I am convinced that the true explanation of this puzzling variation is that incipient albinism has gained a foothold, of such nature that areal restriction of the ear or crown patches is developing, so that a white line results between them. In the crested auklet (*Æthia*) a member of the same family, of the Pacific Coast, such a line has become fixed so that it now forms a characteristic mark of the species. In the case of the "ringed murre," I should expect to see the eye stripe in the young as well as in the adult stage of those individuals which are to have the mark—in other words it is a permanent trait. No doubt the heredity of this white stripe is of some definite sort, and if a recessive character, it may nevertheless in time become common to an increasing number of birds, as this is a colonial species and the possibility of inbreeding is thus increased.

The Neck Patches.—In birds the neck patches extend forward from the breast to meet the crown patch at the occiput and the ear patches at the sides of the head, thence ventrally to include the throat and chin. A study of albinistic pigeons, as previously noted, indicates that the neck patches are two separate areas of pigmentation,

one on each half of the part covered, with an ultimate center at the base of the neck, usually the last spot to remain when the area is much reduced.

In albinistic individuals, that is, those in which restriction of the pigment areas has taken place, the neck patches are usually first reduced at the upper part of the throat, so that a white patch appears from the chin to upper throat, as commonly seen in street pigeons; in others, however, the restriction may be at the posterior end of the patch, so that a white ring develops at the base of the neck.

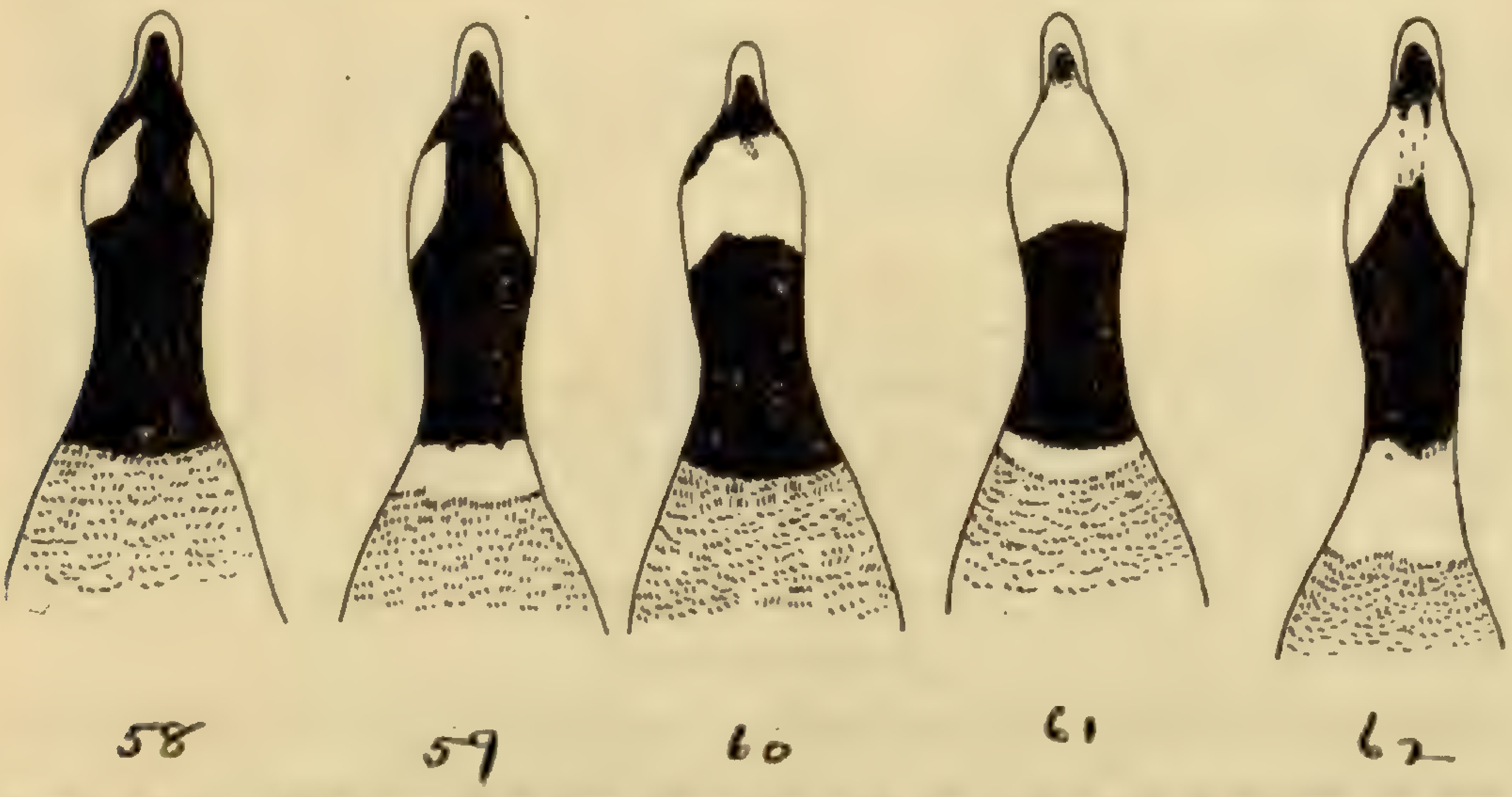
In many birds the neck patches have been much developed as characteristic pigmented areas. Two general categories may be here distinguished: (1) those in which the neck is rather uniformly colored all about, and (2) those in which the ventral portion is heavily pigmented and the dorsal portion much less so. In the latter belong such birds as the black-capped chickadee (*Penthestes atricapillus*) with a black throat but a pale neck. So, too, the golden-winged warbler (*Vermivora chrysoptera*). In this latter category it is probable that a second factor is present, comparable to that producing a centrifugal type of pigmentation in mammals, such for example as in the Himalayan breed of rabbit, which has the end of the nose and the feet black-pigmented, contrary to the usual rule of normal areal reduction where the extremities are the first to become white. That this is a separate category from a physiological standpoint is indicated by its behavior in heredity as worked out so admirably by Faxon (1913) in the case of the Brewster's warbler. He discovered that the black throat as present in the golden-winged warbler is recessive in the cross with a related species, the blue-winged warbler (*Vermivora pinus*), a yellow-throated bird. The offspring of this cross have white throats,—the so-called *V. leucobronchialis*. The black throat patch may be evidence of "centrifugal" pigmentation as defined farther on (p. 53). The essential bilaterality of such a throat patch is

further shown by the fact that one half only may be present as in the golden-winged warbler recorded by Dr. C. W. Townsend (1908).

The first category, in which the neck is uniformly pigmented is illustrated by many of the duck tribe, and probably involves the normal primary patches only. The primary patches are usually restricted first anteroventrally producing a white throat. Often this is carried dorsally so as to form a white ring around the upper part of the neck by the separation of the neck patch from the crown and the ear patches. Again, if the neck patches are restricted posteriorly a white ring is formed at the base of the neck, a common permanent character in many species. The peculiar little goose-like bird—*Nettapus*, of India—has developed this type of marking so that its white neck is encircled by a narrow black ring, and the Labrador duck (*Camptorhynchus*) has a nearly similar mark (Fig. 57). Other ducks, *e. g.*, the mallard, have the white ring at the base of the neck, only.

In an interesting paper on the geese occurring in California, Swarth (1913) has pointed out that in the cackling goose (*Branta c. minina*) there is much variation in the amount of white on the head and neck. Figs. 58 to 62 are traced from a series of photographs illustrating this paper and show the throats of five specimens. The wide range of variation in these specimens indicates to my mind that this goose is in process of reducing the neck patches, and thereby developing a white collar, such as is present in the mallard, and perhaps also a white throat. The usual condition seen in *Branta canadensis* and in so-called normal specimens of *B. c. minina* is seen in Fig. 58. The white cheeks have been developed long ago in the history of the species, in part perhaps by the depigmentation of the ear patches. Now a second change is taking place in one of its subspecies. Thus in Figs. 59, 61 and 62, the neck patches have been reduced posteriorly, a varying amount in each case. In Figs. 60, 61 and 62 these patches have been restricted anteriorly pro-

ducing a white throat, and as sometimes in the pigeon, imperfectly, so that a little island of pigment is cut off just at the chin. It is also obvious from these figures, that reduction may take place either at one end or the other, or at both ends in different individuals. The ultimate development of this line of reduction will produce



FIGS. 58–62. VARIATIONS IN THE DEVELOPMENT OF THE NECK PATCHES IN THE CACKLING GOOSE (after Swarth).

the narrow black collar seen in *Nettapus* previously mentioned. It is worth noting also that in this goose the limits of the neck patch are by their black color sharply defined posteriorly from the gray of the breast which is pigmented from the shoulder patches.

The Shoulder Patches.—The shoulder patches appear to center near the base of the wing, and in reduction produce white remiges, such as appear in a domesticated race of guinea fowl, as well as a white breast. The domesticated guinea fowl often shows this white area in the midline of the breast as the pigment areas fail to spread ventrally. In the normal pattern of wild birds, however, white wings are seldom seen except among certain sea birds. White wing patches are often developed, but these are frequently only bars on pigmented feathers as in the goat-suckers. Probably among small land birds much white in the large wing feathers is a disadvantage,

and so not much developed. It is noticeable that white patches in the wing are often of such a nature that they are concealed through the folding of the wings when the bird is at rest. This accords with my belief that while in flight the bird is unavoidably conspicuous by reason of its motion, and that white patches showing at such times add little or nothing to the disadvantage. In the hairy and the downy woodpeckers (*Dryobates*), a white stripe down the back is developed as part of the pattern, and no doubt as in many mammals, marks the separation between the pigment areas of opposite sides. Centrifugal pigmentation is seen in some species as the kittiwake in which the *outer* primaries are black.

The side patches are commonly continuous with those of the shoulders, and when ventrally restricted, give a white abdomen. Their median separation dorsally, is seen in the hairy and downy woodpeckers as above noted. I have not studied any special developments of these areas, and they are commonly small.

The Rump Patches.—In birds as in mammals the two rump patches pigment the posterior extremity of the body. Their ultimate centers are dorsal and so close together that it is much less common for them to be separated medially than to be restricted laterally. With a slight areal reduction, a separation takes place between them and the side patches dorsally, so that a white area on the rump results. Often this white area represents doubtless a slight restriction of both sets of pigment patches which by drawing farther apart increase the white area along the lower part of the back. In the domestic pigeon much variation may be found, from a condition in which the lower back is wholly pigmented to one in which it is mostly white. The primary break which causes this white patch has been much developed in many groups of birds as a particular mark in the pattern. In many species it is simply of a paler hue than the surrounding parts as in the yellow-rumped warbler (*Dendroica coronata*) or the pine grosbeak (*Pinicola*).

In others the tendency to albinism thus expressed has gone farther so that a pigmentless spot is formed. This white rump patch is present in many unrelated groups of birds in which it has independently arisen through parallel development. Thus it is seen in many of the smaller petrels, in the palm swift, the flicker woodpecker, the white-rumped and other sandpipers, the white-rumped shrike, the European house martin and others. The tail feathers are pigmented by these patches, and among various species show many steps in the process of pigment reduction. As in the domestic pigeon, occasional albinistic individuals show white outer tail feathers, in accordance with the rule that the first pigment reduction takes place at those parts of the primary areas that are farthest removed from the pigment centers. I have seen a white outer tail feather in wild specimens of song sparrows and Lincoln's sparrow and it is occasional in other species. In others again this mark has become developed and fixed as a species character. Thus in the bay-winged bunting (*Poœcetes gramineus*) there is a single white outer feather on each side, in the junco (*Junco hyemalis*) there are two. A white central tail feather is much rarer, but a pure white tail is found occasionally as in the hummingbird, *Leucuria phalerata,* the bald eagle and certain gulls, due to the permanent reduction of the pigment area of the rump at this extremity. I once examined an albino ruffed grouse (*Bonasa*) which was entirely white except for a single feather among the upper tail coverts at the left side of the rump. This blemish in the otherwise pure white bird seemed inexplicable to those who examined it with me, but it merely represents the last remnant of the left-hand rump patch, still persisting though all the other pigment centers were inactive.

It is very interesting that the white rump mark, so commonly found in unrelated groups of birds, is one which is conspicuous in flight only, and the same is true of many of the white tail marks, such as outer white

feathers that disappear when the tail is shut. This points to the conclusion that the development of a white mark which is ever conspicuous is allowed in nature in such cases only where it may be no detriment to the species through rendering it too conspicuous by contrast. Thus the bald eagle or the black-backed gull have nothing to fear from such a banner mark. For small weak-flying birds, however, the case may well be different. Yet even these often show much white and I believe that it would be possible for a species in its phylogeny to develop more and more white if at the same time its habits of watchfulness or other actions developed equally to counteract any disadvantageous result that might accompany the increase. No doubt also a psychic factor is involved, comparable to what among ourselves we call "fashion." Thus a change in action or dress which departs too far from the accustomed appearance is apt to be disliked at first, though in time it may if persisted in, be tolerated and at length accepted. In the development of white markings, for example in the feathers of the tail, it seems likely that a series of small steps must have been made rather than too great and sudden changes. So in the rock pigeon the white of the tail is limited to the outer vane of the outer tail feather. In the turtle dove the outer vane of the outer feather, and the entire tips of the four outer feathers are white. The next step would be to develop an entirely white outer feather and then two (as in the passenger pigeon) and so on. In the sparrows similar steps are shown by the lark sparrow (*Chondestes*) in which the tips only of the outer feathers are white, the bay-winged bunting which has practically all the outer feather white, and a little of the tip of the second, the junco with two outer feathers and part of a third white. No doubt steps such as these must have been passed through by many white-tailed species.

It is difficult to say how disagreeable to their normally colored neighbors, albino birds may be. I have seen an albino robin in the fall of the year with a flock of other

robins and a white-spotted bee-eater with a flock of its brethren, in both cases wholly at peace. This of course was in flocking time when the social spirit is strong. The song sparrow (*Melospiza*) with white outer tail feathers, previously mentioned, was attacked and driven off by another song sparrow. In the *Journal of the Maine Ornithological Society* (Vol. 6, p. 48, 1904), C. H. Clark writes of a pair of albino eave swallows (*Petrochelidon lunifrons*), at Lubec, Maine,

> among a large colony of the common ones who seemed greatly annoyed at the albinos' presence and fought with them until they finally killed one . . . or rather injured it so badly that it died soon after.

I also have a note of a white robin at Montclair, N. J., which in early July, 1909, was seen to be much beaten and driven about by another robin and eventually flew at full speed against a tree and was killed.

Centrifugal Coloration

In addition to the primary pigment patches which I have discussed at some length, and the speckled condition or "English" marking, there is, as I have already intimated, a third condition in which pigment is developed at the extremities or points. It may be called a *centrifugal* type and is almost the reverse of the *centripetal* or "primary-patch" class.

The two latter types of pigmentation may both be found in the same individual, but ordinarily this is not evident except in cases where the primary patches are somewhat restricted in area. It then may become apparent that pigment is present at exactly those points where, in the centripetal type of coloring, it is first to be lacking. Moreover it persists strongly, even though the primary areas are much reduced or largely absent. Curiously this sort of pigment seems almost always to be *black*. Apparently centrifugal pigmentation does not occur in all species. I have never seen any trace of it in dogs. In the house cat it is frequent, however. Thus in Figs.

18 and 19 it appears at the end of the tail. In the former figure the sacral patches are much reduced, though present, and together spread nearly half the length of the tail. The terminal half, or less, of the tail, however, is dark-pigmented, and a break occurs between the two sorts of markings, due to the failure of the centripetal patch to spread so as to unite with the centrifugal area. In Fig. 19 the sacral patches have wholly failed to develop but the centrifugal patch still covers the distal half of the tail. Possibly the dark heel marks in Fig. 16 are patches developed in the same way. In the house cat, a dark or "smutty" nose is often present in contrast to an otherwise white face, or with the ear patches only slightly reduced. In the breed of rabbits known as "Himalayan," the centrifugal pigmentation remains, though the centripetal markings have disappeared, so that it is pure white except for the black nose, ear tips and toes. No doubt, however, it would be possible for the two types of pigmentation to appear in a single individual. This is suggestive of the winter phase of the Arctic hares, in which the black ear tips contrast strongly with the otherwise white pelage. The physiology of the process whereby certain animals acquire a white winter coat is not yet fully worked out. It is curious that in occasional *melanistic* individuals of the eastern varying hare, the black color is retained throughout the winter, instead of being replaced by white—again a persistence of *black* pigment. In dappled gray horses a black patch sometimes appears on the bridge of the muzzle, usually the first place to show white in the restriction of centipetal pigmentation. The feet may also be black. Among certain antelopes a black muzzle mark is similarly present, and in Hunter's antelope (*Damaliscus hunteri*) a white border partly surrounds such a mark. This, I believe, is due to a slight restriction of the ear patches, sufficient to prevent them from reaching the muzzle, and of about the same nature as seen in the blesbok (*Damaliscus albifrons*) in which, through the *absence* of a centrifugal nose patch, the entire

front of the muzzle is white. The white chevron on the muzzle of several antelope (*Strepsiceros, Taurotragus*) is probably the result of a similar restriction of ear patches combined with a centrifugal nose patch, leaving a white line between. The black dorsal stripe seen in many mammals and the black tail tip are probably manifestations of centrifugal pigmentation. The latter mark is common in stoats (*Mustela*) and among those that change to a white coat in winter, as the ermine, the tail tip still remains black. In sundry other genera, as *Genetta*, a black tail tip is part of the normal pattern.

In their paper on albinistic negroes, Simpson and Castle (1913) published some highly interesting photographs of "piebald" individuals. In four persons of one negro family the hair over the median part of the head from the occiput to forehead is pure white, as though due to a restriction of the aural pigment patches. In addition, more or less of the median area of the back, as well as the hands (including much of the forearms) and feet (including the lower part of the ankle) are pigmented. These latter areas may represent centrifugal pigmentation, but it should be noted that this is present in the dermis. Possibly there is a close relation between dermal pigment and that produced in the centrifugal style of pigmentation.

Among birds, the black of the outer tail feathers of the ptarmigan (*Lagopus*) may be comparable. A black area is also sometimes present on the middle of the throat, or as in certain gulls the outer primaries may be black.

This form of pigmentation is not found universally and the conditions governing its appearance are unknown, though its heredity in the "Himalayan" rabbit has been somewhat studied by Professor Castle.

SUMMARY

The principal points of this paper may be summed up as follows:

1. In mammals and birds that normally are com-

pletely pigmented, there are certain definite points of the body from which as centers the tendency to develop pigment in the epidermal structures may become less and less. Outward from each of these centers pigment formation spreads to include very definite areas which in wholly pigmented animals overlap slightly at their borders or are at least contiguous.

2. A reduction in the area covered by any of these primary patches results in a white mark at the line of junction of two contiguous color patches, where no pigment is produced. These white marks between the primary patches are spoken of as primary breaks.

3. Through a study of the breaks in pied individuals of domesticated species of mammals and birds, the boundaries of the primary patches have been determined. These are homologous in the two groups and subject to a certain amount of variation in different types. They are: a median crown patch unpaired, and five paired patches on the opposite sides of the body, which are named from the general areas they cover, the ear, neck, shoulder, side and rump patches. Their limits are more precisely defined under the different species treated.

4. These patches are physiologically independent of each other and may be differently colored in the same individual.

5. Pied patterns among many wild species have been brought about through the areal reduction of these pigment patches in a definite way so that the white markings resulting as breaks between the reduced patches have become fixed and form a permanent part of the normal pattern.

6. In several wild species this development of white markings is shown to be even now taking place, but the amount of pigment reduction is still fluctuating so that the white markings vary much in extent with different individuals.

7. The development of such white markings takes place probably by little and little, so that the departure from

type is not so great as to arouse antagonism against the varying individual on the part of others of its species. Also, the gradualness of the change allows the species to become accommodated to any disadvantage that might concomitantly arise.

8. The converse of this centripetal style of pigmentation is present in many species, and results in pigmentation (commonly black) at the extremities or along lines where primary breaks occur in the centripetal form, namely at the tip of the nose, ears, tip of the tail or the toes; possibly the black dorsal stripe is due also to centrifugal pigmentation. Patterns may develop as in certain antelopes by a white break between patches of the two types.

In conclusion, I wish to express my indebtedness to Professor W. E. Castle for much helpful criticism and advice, and to the Museum of Comparative Zoology for permission to make record of specimens in its study collection.

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SHORTER ARTICLES AND CORRESPONDENCE

THE BEARING OF THE SELECTION EXPERIMENTS OF CASTLE AND PHILLIPS ON THE VARIABILITY OF GENES

Castle and Phillips have recently reviewed the results of six years' work in which they selected for and against "hoodedness" in rats.[1] In "hooded" or "piebald" rats only part of the coat is pigmented; the area of dark (versus white) coat varies greatly in different animals, but tends, in those of medium grade, to cover the head, shoulders and middle of the back, like a hood. Starting with a strain which was probably hybrid, although of unknown ancestry, and selecting during thirteen generations for a larger extent of colored coat ("plus" selection), they succeeded in obtaining animals with a greater and greater area of pigmentation. The average, the mode, and the extremes were raised. Conversely, selection for less pigmentation ("minus" selection) was accompanied by a gradual but decided and continual dimunition in the dark area. "Return" selection also succeeded; that is, plus selection was effective even in a line which was already lighter than the average on account of a previous minus selection, and, *vice versa,* minus selection caused a lightening of a strain that had been made exceptionally dark by a prior plus selection.

Certain crosses proved that more than one factor affecting hoodedness is involved in the difference between the different races. Therefore the production of animals of desired grade by selection may perhaps be explained as a mere sorting out, into different lines of descent, of different combinations of the various factors for hoodedness originally present in the heterozygous ancestors. It is the opinion of Castle and Phillips, however, that this explanation will not suffice to account fully for the continued efficacy of selection in their experiments, and they believe it probable that a factor or factors for hoodedness are undergoing variation of a fluctuating nature.

[1] Castle and Phillips, "Piebald Rats and Selection, An experimental test of the effectiveness of selection and of the theory of gametic purity in Mendelian crosses." Published by the Carnegie Institution of Washington. See also Castle's "Pure Lines and Selection" in *American Breeders' Magazine,* 1914.

A conclusion so radical and so opposed to previous work should not be accepted, however, as long as it remains at all reasonably possible to use instead an explanation in harmony with the results of Johannsen and other investigators. Johannsen dealt with a character—dimensions of seed—which must beyond any doubt have been partially dependent upon a very great many factors, yet he found that selection had no effect whatever after he had separated the different genotypes from one another. Thus he proved the constancy of a great many genes "at one blow"—namely, of all the genes appreciably concerned in seed size. Of course, if there had been a chance for cross-fertilization in his experiments, he, like Castle, would have obtained a result from selection, but this would have been due to recombination, not variation, of genes. All our evidence points to the conclusion that the vast majority of genes are extremely constant, although they differ somewhat in that very slight amount of variation which they do show. For example, in *Drosophila*, although in the case of most genes not more than one mutation has been found, yet in one case (possibly in two or three cases) a locus has mutated three times, each time in a different way, thus giving rise to a system of multiple allelomorphs containing four members. This gene evidently is more subject to mutation than the others, yet this formation of a series of multiple allelomorphs can not even remotely be compared to fluctuating variability, for the three mutations were all large steps (much smaller could easily have been detected), and they were found only during the examination of some millions of individuals in the rest of which the locus was not observed to mutate at all. Some few genes are known, however, which really do change frequently (*e. g.*, that for "variegated" corn), but these cases are extremely rare; moreover, here the degree and nature of the change are fixed, and also, after the change has once occurred the instability of the gene is lost. Thus, in no known case do the variations of a gene among, let us say, several thousand immediate descendants of the individual possessing it, form a probability curve, as neo-Darwinians might perhaps suppose, nor even are any cases known where genes can undergo frequent changes that may vary at all in kind or amount or occur successively.

Let us then inquire into the probability and adequacy of that explanation of Castle and Phillips's results which does not require the assumption that a gene or genes involved change compara-

tively frequently and successively, but which assumes a sorting out of numerous factors. It is now pretty generally accepted by Mendelians that the germ plasm of any of the higher organisms contains a large number of genes, which play various rôles in the numberless processes and reactions of development whereby the egg is transformed into the adult individual. The exact nature and intensity of any one characteristic of this adult organism (*e. g.*, hoodedness in rats) is dependent upon the nature of each of the various reactions which were involved in producing this character, and thus dependent upon all the genes (and environmental factors also) involved in any of those reactions. Now, in an ordinary Mendelian cross, all the individuals are usually homozygous and alike in respect to all but one of the pairs of genes that noticeably affect the character concerned. In such a case, then (so far as differences in environmental influences do not obscure the outcome), one obtains the simple Mendelian results derived from the segregation, at reduction, and recombination, at fertilization, of but this one pair of allelomorphs.

The strain of hooded rats, however, was probably a hybrid between two races of rather remote relationship. When two such races are crossed, the individuals often differ in more than one pair of those factors that affect the character studied, especially if the character is such as to be influenced by a relatively large number of genes. It can not be questioned that some characters are thus determined or influenced by a much larger number of developmental reactions than are others, and such characters will therefore vary more in inheritance, since if a difference exists between two individuals in respect to any given gene, these characters are more likely to be affected than others. Gross size, for example, is a character dependent in this way upon an exceptionally large number of genes, for any gene which influences the size of any organ must affect to some extent the total size. In some other cases in which characters are found to be influenced by relatively many genes, the reason for this is not so evident, *e. g.*, in the case of the red flower-color of flax, or the truncated condition of the wing in some races of *Drosophila*. Here the production of the character may be conceived to be dependent upon some reaction that can be easily modified by various means.[2] For our present purpose we must assume that

[2] It is conceivable that differences in respect to numerous genes have sometimes arisen even in the case of characters not naturally very easily

the character "hoodedness" belongs in this class and that the ancestral hooded rats used by Castle and Phillips were the descendants of a cross involving many genes for that character.

The results of such a cross are of course complicated, for the different pairs of allelomorphs generally can undergo recombination at the reduction division of the hybrid, so that in F_2 or subsequent generations as many different genetic types of individuals are formed as there are possible different combinations of those factors wherein the ancestors differed. Not all these genetic types, of course, will fall into different phenotypes, yet generally there will be a large number of overlapping phenotypes among the progeny.

The larger the number of factors in which the two ancestral lines differed, the larger will be the number of different possible combinations of these factors, and accordingly the smaller will be the chance of any individual having one of those particular combinations necessary to a relatively high or a relatively low intensity of the character. In other words, the larger the number of factors (for one character) for which a population is heterogeneous, the more numerous are the possible different grades of intensity of this character among the different individuals, but the fewer will be the individuals which approach the more extreme grades theoretically possible in such a population.[3] Suppose, for example, that two parents differ in five pairs of factors for hoodedness, which are partially dominant[4] to their allelomorphs and summative in their action. Then in F_2 not one

influenced by diverse means, merely because one of the two races had been subjected to a very long and drastic selection, so that any of those rare mutations which affected that character in the desired direction had in this race been preserved. Selection in such a case, however, would have to involve many millions of individuals.

[3] One extreme, *e. g.*, the "plus," will be rather frequent, however, if all the "plus" factors dominate completely. But in the case of the hooded rats we must assume either that dominance is generally incomplete or that in the case of some factors the "minus" allelomorph dominates in the case of others the "plus," since F_1 rats from a cross of the plus by the minus strain are on the average intermediate in type between these two extremes.

[4] It is of course by no means necessary to assume incomplete dominance of the factors. If dominance is complete (in some cases the "minus" factor may dominate, in others the "plus"), the rigor of selection will be diminished, since heterozygous forms can not be distinguished from homozygous. Therefore, although a somewhat greater number of individuals will be found having the limiting values, it will take longer to bring the average up to the limit.

individual in a thousand will have the most extreme dark or light grade of hoodedness possible. However, by selecting the more extreme individuals, and mating them together, a still more extreme grade of hoodedness may be obtained in F_3 (both as to average and limiting values), and the same process may be continued for a good many generations. The number of generations during which effective selection is possible depends on the number of factors concerned, the rigor of selection, and the amount of inbreeding of brother to sister.

In regard to the latter point, since brother and sister are much more apt to be alike in their genetic constitution than are other individuals, offspring from such a mating are more apt to be homozygous and alike, or, we may say, such offspring will tend to be homozygous and alike in a larger number of factors; then, mating two individuals homozygous for these factors together, there will be much less variation and so less opportunity to continue selection among their progeny. In the case of Castle and Phillips's experiments, however, no such attempt at inbreeding was reported. Here, then, the individuals mated together would be more apt to differ genetically, even though they looked alike (thus, one might be AA bb, the other aA bB), and their descendants would therefore present a larger number of different combinations of factors for the selector. Often a greater effect may be eventually produced in this manner than by inbreeding, for a larger number of combinations of factors are thus produced, some of which may be of more extreme type. The effect would usually be slower, however, since such matings tend to keep the strain heterozygous and are often steps backwards. Cross-breeding, then, will help to explain the relatively slow but long-continued and eventually large effect of selection in Castle and Phillips's experiments, although such a result could also be obtained without cross-breeding if the factors were numerous enough.

The "return selections" also are easily explicable on the multiple factor view. Due to the original difference in so many factors, and the fact that cross-breeding diminishes the tendency to homozygosis which selection favors, the rats were presumably heterozygous even after generations of selection. They would not be as heterozygous as before, of course, and, correspondingly, Castle and Phillips did find less variation in the rats after selection. Yet there would still be a good chance for recombination,

and an alteration in the race could therefore be produced by further selection or by return selection. As we have seen, this is especially true if certain factors are completely dominant, although dominance is by no means a necessary condition.

As a very simple illustration, let us suppose that the "plus" factors A and B dominate over the "minus" factors "a" and "b," respectively, and each increase the pigmented area to about the same extent. To begin with, two moderately hooded individuals, Aa bb and aa Bb, were mated together. They produced 1aa bb—light-hooded, 1aa Bb and 1Aa bb—both moderate, and 1Aa Bb—dark. We first select for dark; mating the dark rats together, 9 darks, 6 moderates, and 1 light, would be produced (F_2). The average color of the offspring has thus been increased by selection (the limiting color, too, if dominance is incomplete). It can be still further increased in subsequent generations. On the other hand, the color can be made lighter again by a "return selection," for if, instead of mating the F_2 or F_3 darks together, we mate the moderates or mate darks with moderates, many of the matings will give offspring lighter, on the average, than in the preceding generation; *e. g.*, Aa Bb by Aa bb gives 3 dark, 4 moderate, 1 light, as compared with the previous 9 dark, 6 moderate, 1 light. In subsequent generations, the average could be brought still lower.

Let us now see whether there is any experimental evidence in support of the multiple factor explanation of Castle and Phillips's results, aside from the fact that it is adequate and is the only one consistent with other work. One point of evidence we have noted—the variability of the rats continued to decrease as a result of selection in either direction. This we should of course expect on the multiple factor view, for selection gradually tends towards homogeneity in a population, even though it may require a long time to produce complete homogeneity. The second and strongest evidence is from crosses.

The crosses show that one of the factors concerned in differentiating hooded rats from wild rats, which are pigmented all over, or from "Irish" rats, which are almost completely pigmented, is "hypostatic." In other words, a rat having the normal allelomorphs of this factor will always be self-colored, or nearly so; one having the other allelomorphs will always be distinctly hooded, although the amount of the hoodedness varies. "Self," as it happens, is dominant, in this case, over hooded.

Thus, on crossing a hooded to a wild or Irish rat, all the F_1 are self (or nearly so); in F_2 there are three selfs to one hooded, but the hoodeds vary in intensity. The question then is, does this variation (so far as it is not due to "environmental" differences) depend upon what other "epistatic" or "modifying" factors for hoodedness may or may not be present, or is there evidence that it depends instead, or in addition, upon a variability of one or more of the factors for hoodedness? As will be shown below, it can be proved that different combinations of modifying factors do occur in the different hooded indiviuals: this being true, there can be no ground for making the unusual postulate that in this case or in the selection experiments a factor or factors concerned undergo variation.

The proof is that when light hooded rats from the minus strain are crossed to wild or Irish rats the hooded rats in F_2 vary much more than did the original strain of hooded rats and average much darker. Obviously, the P_1 hooded rats differed from the wild or Irish in a number of modifiers as well as in the hypostatic factor; moreover, as we should have expected, this difference consisted chiefly in the fact that the wild or Irish rats contained "plus" allelomorphs in place of some of the "minus" modifiers present in the P_1 strain that had undergone minus selection. Thus the F_2 hooded rats, containing various combinations of these modifying factors wherein the two strains differed, varied much more than did the parental strain of hooded rats, and were on the average much darker.

In order to escape this conclusion that modifying factors were involved, Castle and Phillips at first postulated that the reason that the F_2 hooded were darker than the original "minus" strain was because the factor for hooded had in many cases become contaminated by its allelomorph (the factor for self) in the F_1 rats. This is violating one of the most fundamental principles of genetics—the non-mixing of factors—in order to support a violation of another fundamental principle—the constancy of factors. The refutation of their supposition came unexpectedly soon. It would be expected, on the view of multiple factors, that the wild or Irish rats (containing the allelomorph for self in place of the hypostatic factor for hooded) would not possess as many "minus" modifiers as the hooded strain which had been specially selected to contain as many of these as possible; neither would these "self" rats contain as many "plus" modifiers as the

hooded strain which had undergone plus selection (and which so contained nearly all of the plus modifiers originally present in *either* the self or the hooded ancestors). Thus it was to be expected that, just as a cross of self with the minus race gave F_2 hooded rats darker than the original minus strain, so a cross of wild or Irish rats with hoodeds resulting from the plus selection would give F_2 hooded rats *lighter* than those of the plus strain. This result was actually obtained. It was fatal to the idea that the difference between the P_1 strain of hooded rats and the F_2 hoodeds was due to contamination of the allelomorph for hooded with that for self, since such contamination should have resulted in F_2 hooded rats *darker* than those of P_1, not lighter. For wild and Irish rats are both much more extensively pigmented than hoodeds even of the plus strain.

The change in hoodedness from P_1 to F_2 was therefore due to recombinations of the modifying factors wherein the two strains differed. That many such modifiers were concerned is indicated by the evenly distributed variability of the F_2 hoodeds and the fact that very few were as extreme as the hooded grandparents. The same fact is brought out in a cross of the minus with the plus race; here no clear-cut ratios were obtainable, the classification into different genotypes being rendered impossible by the multiplicity of factors (no one of which was hypostatic as in the other crosses). Of course, this knowledge of so many factors being concerned in the crosses helps our interpretation of the selection results decidedly, for the more numerous are the factors concerned, the longer would it be possible to continue an effective selection on the progeny of the hybrids, and the original hooded rats of the selection experiments were admittedly in all likelihood descended from just such hybrids. The exact number and effect of the different factors can not be determined from Castle and Phillip's data, since to do this very special crosses must be made and individual pedigrees kept. Selection experiments can be of little value so long as there are factors for which the individuals may be heterozygous, unless these factors can be accurately followed in inheritance.

Of course, it is quite possible that in the course of these long-continued experiments mutations affecting the hoodedness occasionally happened to arise, especially since it seems likely that this character is dependent upon an unusually large number of genes, for then, as a matter of mere chance, any mutation which

occurred would be more likely to affect it than it would be to affect most characters. It is interesting to note that one such mutation, of a very marked and unquestionable character, was in fact observed. The mutant factor proved to be a strong "plus" modifier, which was almost completely dominant, and itself showed no contamination or variation, so far as could be determined. It arose, as it happened, in the plus strain. A part of the effectiveness of selection may therefore have been due to the occurrence and sorting out of such occasional mutations, but there is no way of telling how many of these took place, or *any* need for assuming them at all in explaining the result. These rare mutations, however, would form a very different phenomenon from such fluctuating or frequent and progressive variation of a gene or genes concerned as Castle postulates. Although the academic possibility of variation of the latter type can not be denied, there is no experimental evidence which can be used to support it, and there is good evidence against it in many individual cases.

It is difficult to believe that this suggestion of Castle and Phillips was not made in a spirit of mysticism, when we consider also their suggestion that the genes may undergo contamination, and especially when we consider the following passage, with which their paper concludes:

> It seems to us quite improbable that the plus mutation could have arisen in the minus selection series. We believe that the repeated selection which was practised had something to do with inducing this change in the plus direction. If one can increase at will the "modifiers" which make the pigmentation more extensive, it does not seem strange that after a time a readjustment should occur within the cell which should incorporate modifiers in that part of the cell which is responsible for the unit-character behavior of the hooded pattern. This would amount to a quantitative change in the unit-character for hooded pigmentation.

To thus suppose that independent genes *fuse* or induce changes in one another, merely because they happen to produce similar *end effects* upon the organism, and in spite of the fact that they usually lie in different chromosomes and are apt to differ from each other as much as do other genes, is utterly teleological.

A paper by A. L. and A. C. Hagedoorn criticizing Castle's work and conclusions, appeared at the same time as the paper of

Castle and Phillips.[5] The Hagedoorns champion the multiple factor hypothesis as an explanation of Castle's results, and also cite certain rather inconclusive experiments of their own to support this point of view. They err, however, in supposing that the factors concerned must be incompletely dominant; as we have seen, this is not a necessary assumption, if we admit that in the case of some modifiers the "minus" allelomorph dominates, in others the "plus." They also err in denying the possibility, on the multiple factor view, of successful "return selection," if inbreeding be strictly followed. In fact they offer this as a test of their point of view. As we have seen, "return selection" would be possible in some cases, even if the animals were inbred; and in Castle and Phillips's experiments, where inbreeding was not followed, "return selection" was certainly very effective.

Finally, papers have recently appeared by MacDowell,[6] in which he gives evidence that certain other cases of inheritance (*e. g.*, head size in rabbits), formerly considered by Castle to support the idea of genic variation and contamination, are probably best interpreted on the view of multiple factors instead. His evidence consists in the fact that the characters concerned are somewhat more variable in the offspring of back-crosses than in F_1, as we should expect on the basis of recombination of multiple factors, but which he believes could not plausibly be explained otherwise.

HERMANN J. MULLER

[5] A. L. & A. C. Haagedorn, "Studies on Variation and Selection," *Zeit. f. ind. Abst. u. Verab.*, 1914.

[6] E. C. MacDowell, "Multiple Factors in Mendelian Inheritance," *Jour. Exp. Zool.*, 1914, and Carnegie Inst. of Wash., 1914.

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SEX-LIMITED AND SEX-LINKED INHERITANCE

PROFESSOR T. H. MORGAN

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DARWIN used the expression "inheritance as limited by sex" to include all cases in which a character is peculiar to one sex. His list of such cases covers in the main the group of secondary sexual characters. Darwin's expression has been contracted to sex-limited inheritance, and is widely employed to-day in the same general sense in which Darwin used the expression. For instance, Bateson in his book "Mendel's Principles of Heredity" includes both horns in sheep and color blindness in man as sex-limited characters.[1]

Now that the inheritance of several of these cases has been definitely worked out, it has become increasingly evident that such characters as color blindness, and hæmophilia in man, the twenty-five "sex-linked" characters in Drosophila, and certain characters in birds and in butterflies follow a law of inheritance that is essentially different from that followed by some of the other cases. It has become necessary, therefore, to recognize two groups of cases that differ fundamentally in regard to their heredity. To one of these groups I have applied the term sex-linked inheritance, and, for the present at least, we may still make use of the older expression sex-limited inheritance (and

[1] See pp. 169–174 in section headed "Heredity Limited by Sex; the Horns of Sheep," where the term sex inheritance limited descent (p. 172) also appears.

sex-limited character) to cover that class of cases (obviously a very mixed one which will be broken up as our knowledge regarding it becomes more certain) that includes largely, as originally intended, the secondary sexual characters.[2] In those cases of sex-linked inheritance, in which the male is heterozygous for the sex factor, the grandfather transmits his peculiarity, through his daughters, to half of his grandsons only; and reciprocally an affected female transmits her peculiarity to all her sons, and, through her sons bred to her daughters, to half of her granddaughters and to half of her grandsons[3]. Moreover the appearance of the character in the female is not exceptional or abnormal, as is sometimes implied in cases like color blindness in man, for, the character can always be transferred from the male to the female by suitable crosses.

On the other hand, there are cases in which a character appears in one sex only—the character is limited, therefore, to the male or to the female. Such cases may be properly called sex-limited, and were so called by Darwin. As typical examples I may cite the horns of certain races of sheep that are present in the ram and absent in the

[2] G. H. Shull has recently said (*Zeit. Ind. Abst. und Vererb.*, XII, 1914, p. 160) that, in his opinion, it would be better to retain the term sex-limited for those cases that I call sex-linked and call other cases secondary sexual characters. This view is not historically in accord with Darwin's usage of the term "limited by sex." This fact, in itself would be a sufficient argument for rejecting Shull's suggestion, but, in addition, the term sex limited is an actual misnomer for the class of cases to which he proposes to apply it. There are cases like the eosin eye of *Drosophila* that differ in the male and female in the same way as do many secondary sexual characters (in fact they are such in a descriptive sense) but nevertheless show sex-linked inheritance. Since a new name is required to express our fuller information in regard to some of the characters that were originally included under the older term, why not begin by adopting suitable and expressive ones.

[3] In those cases in which the female is heterozygous for a sex factor, as in birds and in butterflies, the same principle is involved but the sequence is, in a sense, reversed; thus the grandmother transmits, through her sons, her peculiarity to half of her granddaughters; and reciprocally, the affected male transmits his peculiarity to all of his daughters, and, through his daughters bred to his sons, to half of his grandsons and to half of his granddaughters.

ewe (or else more developed in the ram than in the ewe); the color of butterflies like *Papilio Memnon,* with three types of females; and the dark spot on the abdomen of the male of the bug *Euchistus variolarius.* These characters can not be transferred through the gametes to the female of their own race by any known combination.

Whether one likes or does not like the particular terms used to denote these two classes of cases, the fact remains that there are two such categories, and to ignore their existence is only to make obscure a distinction that is perfectly plain.

Concerning the mechanism involved there is something more that may be said. It has been sufficiently shown in the case of sex-linked inheritance that the sex-linked character follows the known distribution of the sex chromosomes. It is unnecessary to repeat here the abundant evidence in support of this statement. The simplest interpretation of this known relation is that the character is dependent for its realization on the sex chromosomes. I do not mean, of course, that the sex chromosomes alone produce the character but that something in these chromosomes, some "factor," acting in conjunction with the rest of the cell, conditions the character.

On the other hand, in the case of sex-limited characters the facts can not be explained on the assumption that the characters follow the *sex chromosomes.* It is clear that they do not do so. But we can give a consistent interpretation of the facts if we assume that sex-limited characters follow the distribution of the ordinary chromosomes.

Since this relation has recently been not understood and misinterpreted I may be pardoned, I hope, for taking up the question once more.

Wood crossed horned Dorset sheep with hornless Suffolks. The sons had horns, the daughters lacked them. Inbred these gave in the F_2 generation—horned ♂, 3; hornless ♂, 1; horned ♀, 1; hornless ♀, 3. Bateson and Punnett have shown that the results are explicable on the basis that one factor for horns in the male produces

horns but one factor is insufficient in the females. This conclusion was put to the test by breeding an F_1 hornless ewe to a hornless ram. The F_1 ewe should be heterozygous for the factor for horns, and, therefore, when she is bred to a homozygous hornless ram, half of her offspring should be heterozygous for hornlessness and half homozygous for hornlessness. Since half of her sons should have a factor for horns they are expected to develop horns, and this is what occurred. Half of the daughters also should have a factor for horns, but should not develop horns, and this also was true.

It has been recognized *for several years* that this and related cases can not be explained on the assumption that the factors involved are carried by the X or by the Y chromosomes. But we can interpret the statement that one factor for horns is sufficient in the males to call forth horns, but not sufficient in the female "in terms of chromosomes," if a factor for horns is carried by one of the chromosomes other than the sex chromosome. In other words we need only appeal to a mechanism with which we are familiar to cover the results.

The second illustration is furnished by the recent experiments of Foot and Strobell, and since the authors have rejected the chromosome hypothesis as inapplicable to their results, and since in the case of insects the conditions are simplified because castration experiments have shown that the sex glands are not themselves responsible for the secondary sexual characters, we may profitably consider this case even more fully.

In one of the bugs, *Euchistus variolarius,* the male has a black spot on the abdomen. The female lacks the spot. A female of this species was crossed to a male of another species, viz., *Euchistus servus,* having no spot in either sex. The daughters had no spot, the sons had a spot fainter than that of *variolarius*. Inbred these gave, in F_2, 249 females without a spot, 107 males with a spot (developed to different degrees) and 84 males without a spot. The F_1 results show that one factor for spot in the male

suffices to call forth in some degree the spot in the hybrid. Its intensity varies from a condition approaching that in pure *variolarius* to a faint spot (possibly even to no spot at all). The F_1 results show also that a single factor in the female fails to cause the spot to develop in that sex. In the F_1 male the failure of the spot to reach in most cases its full development shows obviously that the same conditions that produce a male that is perfect so far as his sex gonad is concerned, do not suffice to cause the full development of the spot, although the factor for the spot is present in one dose at least. The only confusion that is liable to arise is that in none of the F_2 females did the spot appear, although in some of them there must have been a double dose of spot. But the difficulty is imaginary as a little thought will show. In the first place the female of *E. variolarius* herself does not show the spot, *yet this female must have a double dose of spot if spot is in the X chromosome or in any other chromosome (except the Y).* Foot and Strobell by an elaborate analysis of the case show that the factor can not be carried by either the X or the Y chromosome. It is unnecessary to repeat their argument; for, if the factor were carried by the X chromosome, only half of the grandsons should show it, while, in fact, many more than half of them show it; and it could not be carried by the Y chromosome because the Y chromosome of *variolarius* is not present in the female, hence could not have entered the cross as made. We are concerned then only with a third possibility, viz., that there is something in the female condition itself that is inimical to the development of the spot. *Since neither X nor Y carries the factor in question it must be present in duplex in the female of variolarius (if every gamete must have it in simplex and the experiment shows that this is the case), and since the spot does not show in the female of variolarius, it is obvious that it can not appear in that sex even in duplex. If it be granted that the character is like other Mendelian characters, and the authors' evidence show that it is inherited as are Mendelian characters, the conclusion*

is self evident; for, in demonstrating that all of the gametes of variolarius carry spot the authors actually destroy their own argument.

It only remains to point out some of the different ways in which a factor being present in duplex both in the male and in the female produces its effect only in the male. In some cases it has been shown that the ovary produces some substance that is inimical to the production of certain characters. For instance in fowls and in ducks the presence of the ovary suppresses the development of the male plumage. That the factors for the male plumage are present is shown by its development when the ovary is removed. But in some insects it has been found that neither the ovary nor the testis produces these kinds of substances; for, when the testis or the ovary is removed the secondary sexual characters are not affected. Here the mode of explanation must be different. But the conditions, or complex, or factors that produce the ovary in the female are acting in every cell of the body, and consequently an effect, that is indirectly caused in the fowl or duck, might be directly caused in the insect. For, each cell is a chemical factory. Such a factory may help to produce an ovary and the ovary produce a substance that demonstrably suppresses the male plumage, or the same kind of factory may do similar work through the activity of some other part of the body, or conceivably it may do its work in every cell of the body. This it seems to me is the most reasonable view to take of the matter in the case of the *variolarius-servus* cross. We can express the same thought in symbols by representing the female of *variolarius* by XXAABBCCDDSS, etc., and the male by XYAABBCCDDSS, etc. The chemical interaction between two X's and the rest of the cell is of such kind that it produces a female, and the female complex, as such, is inimical to the development of a spot and favorable for the development of the accessory organs of reproduction and of all secondary sexual characters of the female, while XY and the rest of the cell is inimical to the development

of the acessory organs and of the secondary sexual characters of the female, and favorable for the development of the accessory sexual organs and of the secondary sexual organs of the male. This view is of course compatible with the idea that there may be special factors for these organs in chromosomes other than the sex chromosomes, and the view holds both in a general way and on the special chromosome hypothesis as well.

To assume that all the factors for characters that are shown by the male or by the female must be carried by a sex chromosome *of some kind,* if carried at all by chromosomes, is a travesty of the point of view of those who hold to the chromosome hypothesis as a reasonable working hypothesis to account for Mendelian inheritance. Just as it has been shown that there are factors in the sex chromosomes that affect many parts of the body, that are not concerned with differences of sex; so, on the other hand, the evidence shows that there are factors in other chromosomes that are influential in producing secondary sexual characters.

INHERITANCE OF ENDOSPERM TEXTURE IN SWEET × WAXY HYBRIDS OF MAIZE

G. N. COLLINS and J. H. KEMPTON

U. S. Department of Agriculture

Introduction

In a previous publication,[1] the first and second generation of crosses between sweet and waxy varieties of maize were reported and a tentative explanation of their behavior was suggested. It is now possible to add the results of the third season, which to some extent afford a test of the explanation proposed in our first publication.

The immediate result of crosses between the Chinese variety of maize having a waxy endosperm and varieties with sweet endosperm was the production of seeds having a horny endosperm indistinguishable from that of ordinary field varieties of maize. In the second xenia generation all three kinds of endosperm reappeared in the proportion of 9.20 horny, 3.95 sweet, and 2.85 waxy. This ratio was accepted as a 9:4:3 dihybrid ratio. For although the deviations of the individual ears, individual families and the totals were too large to be ascribed to chance, the deviations were not consistently in one direction and to predicate more complicated formulæ would have necessitated different assumptions for different ears. The only interest in treating the problem in this way would be that of solving a mathematical puzzle, for it would be practically impossible to secure individuals enough to test adequately the validity of the assumptions which it would have been necessary to make.

Admitting, then, that the ratios were only an approximation representing a general tendency, it became of

[1] Collins, G. N. and Kempton, J. H., "Inheritance of Waxy Endosperm in Hybrids with Sweet Corn," Circular 120, U. S. Department of Agriculture, Bureau of Plant Industry, 1913.

interest to learn whether predictions were still possible.

For the purpose of making comparisons easy, the original diagram representing the second xenia generation is here repeated. (See Fig. 1.) The meaning of the symbols is as follows: *S* is the factor for sweet, and *X* the factor for waxy. When both *S* and *X* are present the seed is expected to be horny. Small letters indicate the absence or latency of the factors.

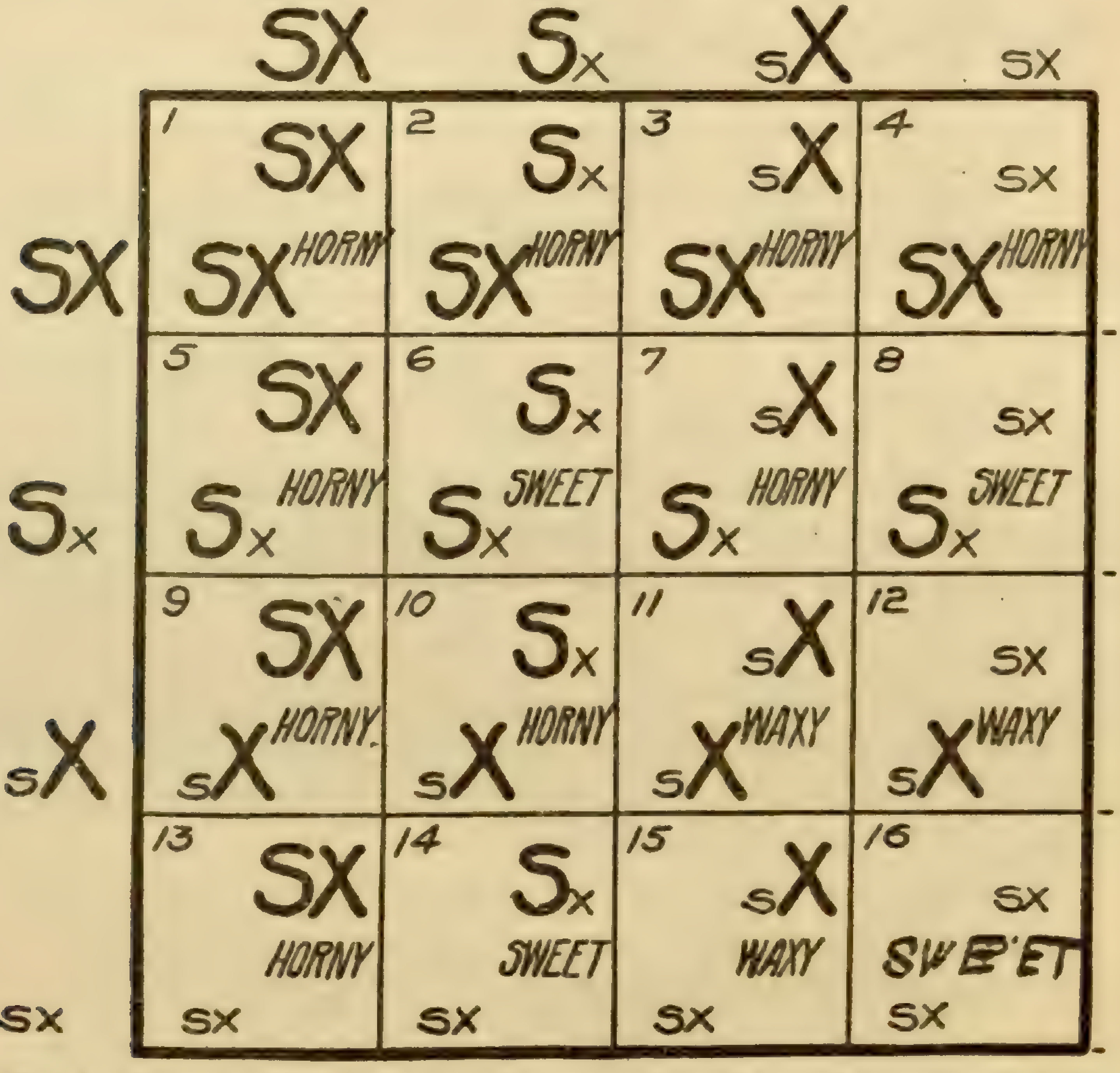

FIG. 1. Diagram showing the gametic composition of second-generation hybrids between waxy and sweet varieties of maize.

Since in both sweet and waxy the alternative factor necessary to produce horny is assumed to be lacking, the gametes produced by sweet varieties are represented by *Sx* and the gametes produced by varieties with waxy endosperm by *sX*. The synthetic horny produced by crossing waxy and sweet is then represented by a combination of

these, or *SxsX*. Assuming a chance recombination of these factors in the gametes derived from these synthetic horny seeds, the gametes will be of four kinds. Both the sweet and the waxy may be present (*SX*) or the sweet may be present without the waxy (*Sx*), or the waxy without the sweet (*sX*), or both may be absent (*sx*). At fertilization each of these kinds of gametes may unite with any one of the four corresponding kinds derived from the other parent, producing 16 zygotic combinations. In the diagram the four classes of gametes from one parent are given in the horizontal row at the top, and the same four classes from the other parent in the vertical row at the left. Each gametic combination from the top is repeated four times in the squares below, while each combination at the side occurs four times in the corresponding horizontal row of squares. Thus each of the squares represents the result obtained by combining the gametes representing the horizontal and vertical rows that intersect at that point. In all cases where both *S* and *X* occur together the seed should be horny, where only *S* occours the seed should be sweet, when only *X* occurs it should be waxy, and in one square (No. 16), where neither *S* nor *X* occurs there is a new combination which the results have shown to be a new type of sweet seed, indistinguishable from ordinary sweet seed but behaving differently when crossed with other types of endosperm.

In accordance with the above analysis the expected results in the third xenia generation were as follows:

	Proportionate No. of Ears.	Proportions of Seed Classes.
Self-pollinated horny.		
	1	All horny
	2	3 horny: 1 sweet
	2	3 horny: 1 waxy
	4	9 horny: 4 sweet: 3 waxy
Self-pollinated sweet.		
		All sweet
Self-pollinated waxy.		
	1	All waxy
	2	3 waxy: 1 sweet

Crosses between different plants from horny seeds.		
	25	All horny
	20	3 horny: 1 sweet
	20	3 horny: 1 waxy
	16	9 horny: 4 sweet: 3 waxy
Crosses between different plants from sweet seeds.		
		All sweet
Crosses between different plants from waxy seeds.		
	5	All waxy
	4	3 waxy: 1 sweet
Crosses between horny and sweet.		
	3	All horny
	6	1 horny: 1 sweet
	1	1 horny: 1 waxy
	2	3 horny: 1 waxy
	2	1 horny: 2 sweet: 1 waxy
	4	3 horny: 4 sweet: 1 waxy
Crosses between horny and waxy.		
	5	All horny
	4	3 horny: 1 sweet
	10	1 horny: 1 waxy
	8	3 horny: 2 sweet: 3 waxy
Crosses between sweet and waxy.		
	1	All horny
	1	All waxy
	2	1 horny: 1 sweet
	2	1 horny: 1 waxy
	2	1 sweet: 1 waxy
	4	1 horny: 2 sweet: 1 waxy

Third Xenia Generation

Four of the ears bearing second xenia generation seed were selected for planting in 1913, one self- and one cross-pollinated ear from each of the two hybrid families Dh 216 and Dh 221. These families were selected because in 1913 the family Dh 221 showed the greatest deficiency of sweet seeds and Dh 216 was the only family that showed sweet seeds in excess of the expected. The three classes of seeds from each of the ears were planted separately.

Unfortunately as the result of an accident crosses were not made between the plants grown from the different classes, but a total of 77 selfed ears were obtained, a num-

ber sufficient to indicate whether the initial assumption regarding the gametic compositions was of value in arranging the observed facts.

Progeny of Sweet Seeds

Sweet seeds were assumed to result from squares 6, 8, 14 and 16. It will be seen that in none of these is there any factor other than *S* and since the absence of both factors, as in square 16, is also assumed to produce sweet, we should expect nothing but all sweet ears from self-pollinated plants grown from sweet seeds.

Seventeen self-pollinated ears were secured from plants grown from sweet seeds. All the seeds of these ears were sweet with the exception of one waxy seed. This one waxy seed was colored and since it occurred on an ear from a white sweet seed that otherwise produced only white sweet seeds, the exception may reasonably be ascribed to accidental foreign pollen.

Progeny of Waxy Seeds

Waxy seeds were assumed to have resulted from the combinations shown in squares 11, 12 and 15. Seeds from square 11 should produce only waxy seeds. Squares 12 and 15 should produce ears with waxy and sweet seeds in proportion of 3 waxy to 1 sweet. There should, therefore, be one all waxy ear to two with both waxy and sweet seeds. There were in all 29 ears from waxy seeds, 11 of which were all waxy and 18 with both waxy and sweet seeds. The numbers are small but at least both kinds of ears were secured and the proportion does not violate the original assumption. The 18 ears with both waxy and sweet seeds all produced them in approximately the 3:1 ratio. The numbers are given in Table I. The totals with 3,154 seeds indicate that if there is a deviation, it is almost certainly less than 2 per cent.

All the sweet seeds that occur on ears grown from waxy seeds are assumed to belong to the new class of sweet seeds corresponding to that represented in square 16.

Plantings of such seeds are being made for comparison with the ordinary class of sweet seeds having the same ancestry. These are represented by the sweet seeds occurring on ears having horny and sweet seeds.

TABLE I

WAXY SEEDS SELF-POLLINATED. EARS SHOWING WAXY AND SWEET SEEDS. EXPECTED: 25 PER CENT. SWEET

Parent Ear	Pedigree Number	Total No. Seeds	No. Waxy Seeds	No. Sweet Seeds	Per Cent. of Sweet Seeds	Deviation ÷ Prob. Error
Dh 216-1 (Cross-Pollinated)	1938	301	216	85	28.2 ± 1.7	+1.9
	1939	112	85	27	24.1 ± 2.7	− .3
	1940	264	202	62	23.5 ± 1.8	− .8
	1942	18	14	4	22.2 ± 6.6	− .4
	1943	349	258	91	26.1 ± 1.6	+ .7
	1949	149	100	49	32.9 ± 2.6	+3.0
	1950	138	103	35	25.4 ± 2.5	− .2
Dh 216-2 (Self-Pollinated)	1972	389	302	87	22.4 ± 1.4	−1.9
	1973	187	136	51	27.3 ± 2.2	+1.0
	1974	174	138	36	20.7 ± 2.1	−2.0
	1975	85	67	18	21.2 ± 3.0	−1.3
	1976	34	21	13	38.2 ± 5.6	+2.4
	1977	313	232	81	25.9 ± 1.7	+ .5
	1978	109	79	30	27.5 ± 2.9	+ .9
Dh 221-2 (Self-Pollinated)	1994	136	105	31	22.8 ± 2.4	− .9
	1995	155	116	39	25.2 ± 2.3	+ .1
	1996	51	31	20	39.2 ± 4.6	+3.1
	1997	190	146	44	23.2 ± 2.1	− .9
	Total...	3,154	2,351	803	25.5 ± .5	+1.0

PROGENY OF HORNY SEEDS

From the horny seeds the expected results are more complicated. They may be tabulated as follows:

1 ear (Square 1)	with seeds all horny
2 ears (Squares 2 and 5)	with seeds 3 horny: 1 sweet
2 ears (Squares 3 and 9)	with seeds 3 horny: 1 waxy
4 ears (Squares 4, 7, 10 and 13)	with seeds 9 horny: 4 sweet: 3 waxy.

Ears were, therefore, expected in the proportion of 1 all horny ear, 2 with horny and sweet seeds, 2 with horny and waxy seeds and 4 with all three classes. Thirty ears were secured from seed classed as horny. These ears were distributed as follows: 1 all horny, 5 with horny and

sweet seeds, 3 with horny and waxy seeds, 19 with horny, sweet and waxy seeds and *2 all sweet.*

The two all sweet ears are entirely outside the expected. Their appearance may be explained on the assumption that seeds classed as horny in 1912 were in reality sweet. No microscopical examination of the starch was made and the seeds were classified on their appearance, wrinkled seeds being classed as sweet and smooth seeds as horny. The separation of horny from sweet seeds is more difficult to make than waxy from either horny or sweet.[2]

There were, however, very few doubtful seeds in the second xenia generation and in suggesting this interpretation, we may with some propriety be accused of attempting to explain away "green balls."[3]

The two all sweet ears were descendants of an ear Dh 221–2, which showed an excess of horny seeds and a deficiency of sweet. The expected number of sweet seeds in Dh 221–2, which had a total of 493 seeds, was 123 and only 106 were classified as sweet. If this deviation resulted from a faulty classification, that is, if some of the sweet seeds failed to show the characteristic wrinkled exterior, we might expect that about 17 of the 300 seeds classed as horny would produce ears with all sweet seeds. Eleven of the ears secured from horny seeds in 1913 were descendents of this ear.

The remaining 28 ears from horny seeds are distributed among the 3 classes in reasonably close agreement to the expected. Measured by Pearson's formula for the goodness of fit,[4] it appears that such a deviation might be expected once in about twenty times.

[2] The difficulty of distinguishing between sweet and starchy seeds in crosses where the starchy variety has small seeds has been pointed out by East and Hays, "Inheritance in Maize," Bull. 167, Conn. Ag. Exp. Sta., 1911, p. 40.

[3] Pearson, K., and Heron, D., "On Theories of Association," *Biometrika,* IX, pp. 309–314.

[4] *Phil. Mag.,* Vol. L, 1900, pp. 157–175. The application of Pearson's formula to data of this kind was called to our attention by Mr. G. Udney Yule.

The three ears with horny and waxy seeds produced these classes in the expected 3:1 ratio. The numbers are given in Table II.

TABLE II

HORNY SEEDS SELF-POLLINATED. EARS SHOWING HORNY AND WAXY SEEDS. EXPECTED: 25 PER CENT. WAXY

Parent Ear	Pedigree Number	Total No. Seeds	No. Horny Seeds	No. Waxy Seeds	Per Cent. of Waxy Seeds	Deviation ÷ Prob. Error
Dh 216–2 (Self-Pollinated)	1962	327	247	80	24.5 ± 1.6	.3
Dh 221–2 (Self-Pollinated)	2000	312	235	77	24.7 ± 1.6	.2
	2007	121	82	39	32.2 ± 2.9	2.5
	Total...	760	564	196	25.8 ± 1.1	.7

Four of the five ears that produced horny and sweet seeds were also as close as could be expected to the 3:1 ratio. The fifth, however, Ped. 1965, with 249 seeds, had only 19 sweet seeds or 7.6 per cent. The numbers are given in Table III. The only explanation that can be

TABLE III

HORNY SEEDS SELF-POLLINATED. EARS SHOWING HORNY AND SWEET SEEDS. EXPECTED: 25 PER CENT. SWEET

Parent Ear	Pedigree Number	Total No. Seeds	No. Horny Seeds	No. Sweet Seeds	Per Cent. of Sweet Seeds	Deviation ÷ Prob. Error
Dh 216–1 (Cross-Pollinated)	1965	249	230	19	7.6 ± 1.1	16.0
Dh 216–2 (Self-Pollinated)	1979	442	344	98	22.2 ± 1.3	2.2
Dh 221–1 (Cross-Pollinated)	1988	160	121	39	24.4 ± 2.3	.3
Dh 221–2 (Self-Pollinated)	2003	175	134	41	23.4 ± 2.1	.8
	2008	179	141	38	21.2 ± 2.1	1.8
	Total...	1,205	970	235	19.5 ± .8	6.9

offered in connection with this exceptional ear is that suggested for the occurrence of the two all sweet ears among those grown from seeds classed as horny, namely, the existence of sweet seeds which failed to show a

wrinkled surface. This explanation is rendered less probable, however, by the unusual behavior of the aleurone color in this same ear. In the previous discussion the aleurone color has not been considered. To treat of the aleurone color would naturally lead to the question of correlation between that character and endosperm texture, a subject which in these crosses is very complicated and for the treatment of which the results thus far obtained are inadequate. It may be said, however, that with the exception of Ped. 1965 the proportions of colored to white seeds in all the ears bear out the assumption that the inheritance of the aleurone color is governed by two factors, both of which must be present to produce color. In Ped. 1965, however, which was grown from a colored seed, only 23 of the 249 seeds were white. The colored and white seeds are beautifully distinct with no intermediate or doubtful seeds. The ratio of 9.2 per cent. white might be explained as an approximation to the dihybrid ratio of 6.25 per cent. but we must then admit that instead of both factors being necessary for the development of color either factor alone may produce color.

The 19 ears from horny seeds that showed all three classes are assumed to have the same gametic composition as the original second xenia generation, previously reported. The numbers are given in Table IV. The last column of the table gives the odds in 1,000 that deviations equal to those observed are not chance deviations from the expected proportions, as calculated by Pearson's formula. Thus in Pedigree 1953 the odds are 809 to 191, or practically 4 to 1, that the deviation is not the result of chance.

As in the original ears, the approximation is sufficiently close to render futile any attempt to predicate a different arrangement of factors, but many of the deviations are too large to be ascribed to chance. In the totals the sweet class is too low and the waxy too high, in fact there is no significant difference between the totals for these two classes. The deviation from the expected is, however,

largely the result of two ears Ped. 1954 and 1967, and if the explanation suggested for the two all sweet ears from horny seeds is admitted, it may also account for the deviation in these two ears. In both ears the deficiency of sweet seeds is accompanied by an excess of horny seeds, while in neither ear is there a significant excess of waxy seeds.

TABLE IV

HORNY SEEDS SELF-POLLINATED. EARS SHOWING ALL THREE CLASSES. EXPECTED: 56.25 PER CENT. HORNY, 25 PER CENT. SWEET 18.75 PER CENT. WAXY

Parent Ear	Pedigree	Total No. Seeds	Horny Seeds		Sweet Seeds		Waxy Seeds		Chances in 1000 that the Deviation is not Accidental
			No. Expected	No. Observed	No. Expected	No. Observed	No. Expected	No. Observed	
Dh 216–1 (Cross-Pollinated)	1953	39	22	26	10	5	7	8	809
	1954	350	197	236	87	36	66	78	999+
	1955	198	111	103	50	55	37	40	470
	1956	69	39	42	17	11	13	16	777
	1957	148	83	74	37	42	28	32	664
	1958	176	99	100	44	41	33	35	133
	1963	540	304	289	135	133	101	118	832
	1964	70	39	44	18	8	13	18	983
	1966	170	96	101	42	35	32	34	524
	1967	158	89	108	39	23	30	27	995
Dh 216–2 (Self-Pollinated)	1980	35	20	16	9	11	7	8	486
Dh 221–1 (Cross-Pollinated)	1985	258	145	131	65	73	48	54	784
	1986	120	67	72	30	25	23	23	443
	1987	375	211	201	94	92	70	82	716
Dh 221–2 (Self-Pollinated)	1999	77	43	42	19	16	14	19	676
	2001	27	15	15	7	7	5	5	0
	2002	118	66	71	30	29	22	18	426
	2004	134	75	81	34	29	25	24	455
	2009	79	44	48	20	10	15	21	979
	Total	3,141	1,767	1,800	785	681	589	660	999.99

With these two ears excluded the deviation in the total for the remaining 17 ears may be ascribed to chance. Tested by Pearson's formula such deviations might be expected once in about 50 times.

Conclusions

The immediate (xenia) result of crossing varieties of maize having sweet and waxy endosperm was the production of seeds with a horny endosperm resembling that of ordinary field varieties. In the second xenia generation all the ears contained seeds of the three classes, sweet, waxy and horny, in fairly definite ratios. The data were arranged in accordance with the Mendelian formula corresponding most nearly to the observed numbers.

The third generation, like the second, gave results sufficiently close to dihybrid ratios to render unprofitable the assumption of more complicated ratios. There are, however, deviations from the expected numbers of too great magnitude to be ascribed to chance.

The ratios of waxy to non-waxy seeds were regular as far as the conditions of the experiment could determine, except for a slight excess in the number of waxy seeds in nearly all the ears in which all three classes appeared (Table IV). A deviation in number of waxy seeds as large as that shown in the total would not be expected to occur as the result of chance more often than once in one thousand times.

The ratios between sweet and horny, while approximating the predicted ratios, show numerous irregularities. Wherever there is a significant deviation in the number of sweet seeds, the observed number is below the expected. Reasons are advanced for believing that the deficiency of the sweet class may result from a failure of some sweet seeds to develop a wrinkled exterior rather than from any irregularities in segregation.

The results show the value of representing the characters by gametic factors. This method provides an orderly arrangement of the facts of heredity thus far observed with respect to these characters and makes possible fairly accurate predictions regarding the genetic behavior of the various seed classes.

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A STUDY OF VARIATION IN THE APPLE

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As a rule the subject of variation in the several characters of the apple has been given but incidental attention, and that usually in connection with the study of other problems. As a result the literature on the subject is of a fragmentary character consisting usually of a few observations here and there in papers dealing with other subjects.

It is perhaps worth while to note a few of the investigations which have thrown some light in an incidental way upon the causes of variation in apples. In fertilizer tests which were made at the New York Geneva station[1] and elsewhere, no well-defined and uniform influence of the various elements of plant food upon the color could be detected, though the New York station reports more decided results in seasons when the natural conditions were unfavorable to the development of highly colored fruit. In the comparison of tillage and sod mulch in an apple orchard, also conducted by the New York Geneva station,[2] it was found that the fruit from an orchard in sod was more highly colored and matured one to three weeks earlier than that from the tilled plot, though the latter was better in quality and kept four weeks longer in common storage. The influence of the stock upon the character of the fruit is a matter of much obscurity, the investigation of which presents such difficulties that it has received little attention. The effect of pollination also is still far from settled. It was thought at one time that the characters of the fruit were profoundly modified by the pollen received by the blossom. The data on this

[1] Bull. 289.

[2] Bull. 314.

subject have been collected by Munson,[3] who found that evidence that the pollen has any direct effect upon the fruit is largely lacking. Aside, then, from indirectly modifying the size of the fruit, the influence of the pollen, in so far as our present knowledge goes, may be left out of account in a study of apple variation.

Without doubt the most noteworthy contributions to the knowledge of apple variation are the recent papers by Shaw, of the Massachusetts station, and Stewart of the Pennsylvania station. Shaw's first paper, which appeared in the Massachusetts station report for 1910, deals entirely with the variation of the Ben Davis apple. In comparing specimens grown in a number of widely separated localities it was noted that variations due to climatic condition were strongly marked and affected practically all characters of the fruit. Modifications of form were especially noticeable The depth of coloration was looked upon as correlated with latitude, being pink in the specimens from Arkansas and deep crimson in those grown farther north. The amount of overcolor seemed to be controlled by local conditions. The color was especially good in the apples from the Pacific coast and those from Colorado, Pennsylvania, and Indiana. In a given orchard temperature appears to be the most influential factor governing size. The flesh was notably white in the fruit from Colorado. The apples from Colorado and California were less firm than those from other localities. The southern-grown specimens were more juicy and of better quality than those from the north, which were apt to be dry, hard, flat, and sometimes astringent. It appears that a mean temperature of at least 60° F. for the growing season is required for the satisfactory production of the Ben Davis. The poor quality of the northern-grown specimens is apparently due to a lack of sufficient heat to properly develop the fruit.

In Shaw's second paper in the Massachusetts station report for 1911 the fact is emphasized that the grower

[3] Me. Sta. Rept. (1892), pp. 29–32.

should choose those varieties which he can grow to the highest degree of perfection under his conditions of soil and climate. The causes of variation are summarized, giving special attention to the influence of temperature as a factor in the distribution of apple varieties. The northern limit is regarded as fixed by the lowest temperature which the tree will stand, while the effect of summer heat upon the development of the fruit is looked upon as limiting the distribution southward. The elongation of the fruit was found to be correlated with a low temperature for two or three weeks after blooming. A low summer temperature produces greater acidity, higher content of insoluble solids, greater astringency, smaller size, and scalding in storage. The extent of coloration was regarded as decreasing from the center of distribution in passing either north or south, while the intensity of coloration was considered greatest in high latitudes and altitudes. Excessive summer heat results in uneven ripening, premature dropping, rotting on the tree, poor keeping quality, lack of flavor, mealiness, less intense color, and smaller size. For each variety there is a mean summer temperature at which it reaches its highest development.

It will be noted that Shaw's method of investigating the problem consisted in securing fruit for comparison from widely separated localities and attempting to correlate the various characters with the conditions of production. Stewart, on the contrary, confined his study to apples grown in one locality and noted the effect of modifying one at a time those factors within his control. This is the more scientific method of procedure, but has the disadvantage that the variations are far less striking and a smaller number of factors can be studied. An account of Stewart's experiments and the results so far attained is found in the reports of the Pennsylvania station since 1907. These papers deal largely with the effect of fertilizers and different cultural methods on the yield, color, size and growth of the apple. The various factors influ-

encing these characters are enumerated and the results are given of the studies made of them. It is noted that the factors are so interrelated that the best conditions for producing one effect are often injurious in some other direction and that the chief problem in orchard management is a proper balance of the various factors. An "optimum principle" is recognized, according to which plant growth and development increase as the most distant essential factors approach the optimum. The factor farthest from the optimum, therefore, whether below or above, may control the results from a crop

OUTLINE OF THE EXPERIMENT

Since the season of 1912 was one of full crop in nearly all centers of apple production, conditions were especially favorable for the study of variation in this fruit. The writer accordingly obtained specimens for study and comparison grown in a number of localities under quite dissimilar conditions. The method employed was therefore that of Shaw, as pointed out in the last paragraph, rather than that of Stewart. The study has been pretty largely confined to Washington-grown apples, though a few have been obtained for purposes of comparison from the east and middle west. The formal investigation of the problem has been carried on but a single season, which is entirely too brief a study to demonstrate conclusively all points touched upon. The conclusions reached, however, are strongly supported by many observations in various localities extending over a number of seasons, and are so suggestive of further lines of study as to justify a report at this time.

In carrying on this investigation the aim has been to secure as much information as possible regarding the conditions under which the fruit was grown. The endeavor has been to get into communication with the growers and obtain from them through correspondence data regarding the character of the soil, rainfall, irrigation, elevation, exposure, temperature, age of trees, fertilization and

cultivation. The chief line of observation had to do with the variations which occur in the different samples of the same variety as obtained from different sources. To get at this side of the problem, careful observations were made as to the condition of the apples, and their various characters were recorded in a complete technical description of each sample for the purpose of making a comparative study of the samples of the several varieties. In addition to this written description, photographs were made showing typical specimens in various positions and when cut in cross and longitudinal sections. In general it may be said that variations are found in the form, size, color, internal structure, texture, flavor, quality, specific gravity, chemical composition, time of ripening, and keeping quality. The attempt is made to correlate these characters with the conditions of growth in so far as they are known and to work out the law of the relation of environmental factors to the characters of the fruit.

The following apples were made use of in the study: Arkansas, one sample; Arkansas Black, one sample; Baldwin, eight samples; Ben Davis, nine samples; Delicious, three samples; Esopus, seven samples; Gano, seven samples; Grimes, seven samples; Jonathan, eight samples; Lawyer, one sample; McIntosh, one sample; Northern Spy, seven samples; Rhode Island Greening, three samples; Rome, eleven samples; Stayman, five samples; Tompkins King, four samples; Wagener, six samples; White Peamain, three samples; Willow, one sample; Winesap, ten samples; Winter Banana, one sample; Yellow Bellflower, four samples; Yellow Newtown, seven samples; and York Imperial, two samples, making a total of 117 samples embracing 24 varieties. These apples were obtained from fourteen localities in the state of Washington and also from one locality in each of the following states: New Hampshire, Indiana, Missouri, New York, and West Virginia.

Before leaving the preliminary portion of this paper the writer wishes to express his appreciation of the aid

received from those who have helped in various ways in the investigation. Thanks are due to the members of the staff of the department of horticulture for suggestions and encouragement, to the members of the library staff who have rendered aid in the study of the literature of the subject, to Mr. Geo. A. Olson, chemist of the experiment station, who has analyzed the various samples of Grimes, Jonathan, Yellow Bellflower, and Winesap, and finally to the various fruit growers and others who have cooperated in securing the fruit and have furnished notes on the conditions of production. To all these the writer takes pleasure in acknowledging his gratitude and indebtedness.

Environmental Factors

Aside from small individual differences, better called fluctuations than variations, and other more striking modifications of comparatively infrequent occurrence and obscure origin, which it is customary to explain as bud variations, if, indeed, the application of a name to a phenomenon can pass as an explanation, it is quite generally recognized that variation in any variety of fruit is due to the operation of external influences. A knowledge of the various factors which make up the environment and their influence upon plant life is necessary to an intelligent study of variation. It should be noted, however, that this influence is not necessarily the same with plants propagated vegetatively as with those grown from seed. In the latter case certain modifications of an adaptive nature which enable the plant to fit in more perfectly with its surroundings are apt to persist, while less favorable modifications tend to disappear by the elimination of the individuals possessing them. In the former case, on the other hand, the modifications observed are the direct result of the conditions, unaffected by selection, and whether desirable or not they persist as long as the environment is unchanged and the vegetative propagation is continued, unless, indeed, the environment is so unfavorable that the

changes induced are pathological in nature and the plant can not survive.

Perhaps the most important factor to which plant life is subjected is the moisture relation. This may be determined by the amount of moisture actually present or by the modifying influence of other coexistent factors which interfere with the availability of the moisture and the capacity of the plant to make use of it. Among such indirect influences may be noted the modifying effect of temperature upon the rate of absorption and transfer of moisture, the presence in the soil of certain salts or humic acids which interfere with the osmotic activity of the roots, and certain atmospheric conditions favorable to rapid transpiration. In such cases care is necessary to determine which is the direct and which the indirect cause of the modifications. If it is borne in mind that many factors cause variation through their influence on the moisture supply confusion may often be avoided.

The temperature relation is much more obscure than the moisture relation in its effect upon plant growth. Heat, being a molecular phenomenon, acts directly upon the protoplasm and its effects are therefore physiological. It is now pretty well understood that heat alone is incapable of modifying plant structure, but acts indirectly through other factors and the functions of the plant. The direct effect of temperature is limited very largely to its influence upon the rate and amount of development. A slight difference in the average temperature of the growing season influences greatly the relative development of apple varieties. The accompanying table gives the mean monthly temperature during the growing season at Geneva, N. Y., and Pullman, Wash., since the establishment of the experiment stations at those points, as well as the mean for two years at White Salmon, Wash.

Locality.	April	May	June	July	Aug	Sept.	Oct.	Aver.
Geneva, N. Y........	44	57	67	71	69	63	50	60
Pullman, Wash.......	47	52	59	66	66	58	48	57
White Salmon, Wash..	50	56	63	70	67	60	53	60

The difference in the development of certain varieties of apples at these places will be noted later. It will be seen that the season opens slightly earlier in Pullman than in Geneva and closes at about the same time. It would appear, therefore, that the better development of most varieties at the latter station is due rather to the higher temperature than to a difference in the length of season. At White Salmon the season is considerably longer than at either of the other stations, while the temperature from May to September is intermediate.

Latitude and altitude are frequently mentioned as important factors in the modification of varieties. These, however, are not primarily factors, but depend for their influence upon the effect of other factors, which in turn are influenced by the location. Differences in altitude especially result in marked changes in climate often in places geographically near together.

The light relation is of much importance to the fruit grower. It is clearly evident that the development of color in apples is largely dependent upon the sunshine, and quality also may be affected through the production of sugars. Both intensity of insolation and duration of the daylight must receive consideration. In general, tropical, arid or alpine situations are characterized by high insolation, while a long period of daylight during the summer months is a factor in northern latitudes.

The effect of atmospheric influences is largely indirect. It has already been noted that the condition of the air may modify the moisture relation through its effect upon transpiration, thus dryness, high temperature, and rarification all favor evaportion, and this effect may be increased in windy situations. Atmospheric pressure is a factor of importance in high altitudes.

The soil may be of importance as a factor in causing variation through either its chemical composition or its physical properties. The former leads to a consideration of the influence of fertilization, the latter to the effect of different methods of culture. Here again other factors,

and especially the moisture relation, have an important bearing, since one of the primary results of cultivation is the conservation of the soil moisture. There is no doubt that the nature of the soil greatly affects the crop and the matter has been given much study. The intimate association of other factors, however, makes it somewhat difficult to pick out those influences for which the nature of the soil is directly responsible.

The influence of other organisms includes not only a consideration of the effect of insect and fungus pests but in the broad sense embraces such items as pollination, pruning and thinning, intercrops, cover-crops and planting distance. Human agencies, including all operations of orchard management, might properly be included here. Many of these are, of course, indirect, exerting an influence through their effect upon some other factor.

The Law of the Optimum

Having enumerated the chief external influences to which plants are subjected during their period of development and to which variation is largely due, the question naturally occurs whether there can be formulated any basic principle or law which will express the manner in which plants react with the environment. Such a law would be of use not only in the study of variation, but would shed much light on the adaptation of plants to new environments. It would constitute a unifying principle whereby isolated facts and disconnected observations appear in proper relation and perspective. Though a discussion of this subject might logically be delayed until after the characters of the several varieties and their modifications have been noted, it is thought most fitting to introduce the statement at this point and examine the fruit in the light of such generalizations as it has been possible to make.

A plant can live and perform its functions only within certain intensities of the various factors of the environment. The degrees of intensity beyond which activity

ceases are known as the *zero points*. The plant does not necessarily die at once, but passes into a dormant state. If the intensity becomes still more unfavorable a point is finally reached at which death occurs. The minimum degree of intensity of a factor at which the plant may remain active is known as the *lower zero point*, while the greatest intensity is called the *upper zero point*. With some factors these points are wide apart, so that, other conditions being favorable, the plant will continue to develop after a fashion at any but the most extreme intensities of such factors. With other factors the limits are comparatively narrow. A plant will reach that degree of development only which is permitted by that factor which is in the least favorable degree of intensity. Such factors are called *limiting factors*. In passing from one zero point toward the other, a point is finally reached at which any given function of a plant reaches its highest state of activity. This point is known as the *absolute optimum* for that function and may not correspond to the most favorable intensity of that factor for the performance of the other functions of the plant. The point of intensity of a factor at which all the functions of the plant are performed to the best advantage is termed the *harmonic optimum*. If each factor is of an intensity corresponding to the harmonic optimum, the plant is in a condition of equilibrium known as the *ecological optimum* and will reach the highest state of activity of which it is capable.[4]

As the life of a plant is made up of various functions, so its structure is made up of a number of organs having various characters. These characters are the result of development, which in turn is dependent upon the performance of the several functions of the plant under the influence of those external conditions which make up the environment. If a factor of the environment is modified in its intensity, the balance of the functions of the plant is disturbed and the plant reacts to its changed environment by a modification of its functions which may result

[4] Schimper, A. F. W., "Plant Geography."

in a different kind of development, or in other words a variation. Having observed the close connection between the characters and the functions of the plant, we may now inquire whether the former maintain a relation to the environment similar to that maintained by the latter. Putting aside generalizations for the present and confining attention to the apple, it is to be noted that both Shaw and Stewart foreshadowed such a relationship in the papers already noted. Neither, however, carried the analysis far enough to formulate a rule of general application, though Stewart came near doing so. Shaw recognized that the highest perfection in any given variety could be attained only under the most favorable summer temperature. Stewart applied this idea to other factors than temperature in his "optimum principle," which is "that plant growth and development increase as the most distant essential factors approach the optimum." His failure to recognize the connection between the various factors of the environment, on the one hand, and the separate characters of the apple, on the other, may be accounted for by the fact that his investigations dealt only with fruit grown under slightly modified conditions, which resulted only in such slight variations that the independent modification of the separate characters escaped notice.

In examining various samples of apples produced under the influence of quite dissimilar combinations of environmental factors, the writer has many times noted the modification of certain characters more or less independently of others. It is true that characters are often found to vary together through a relationship of direct or inverse correlation. Such cases, however, are possibly as often due to the response of the various characters to the same factor of environment as to any direct connection between the characters, though the latter no doubt exists in many cases. Keeping in mind these facts and also the close relationship of function and character, the writer has formulated a principle which he believes is of general application not only to apples but to other horticultural

crops and perhaps in a degree to all plant life. For this generalization, which expresses the relationship of characters to environmental factors the name "Law of the Optimum" is proposed.

This law may be stated as follows: For any given variety there is for each character a certain intensity of each essential factor of the environment at which, other conditions remaining the same, that character reaches its highest development. When all essential factors are in a condition of optimum intensity for any character, that character will reach the most perfect development of which it is capable. A modification of the intensity of any such factor either above or below the optimum will be accompanied by a less perfect condition of the character concerned. The optimum intensity of a factor may be wide or narrow in its limits and the optimum for one character may or may not overlap the optimum for others. A variety will be at its best when grown in an environment the factors of which are as near as may be to the optimum intensity for all characters. Under such circumstances the variety is in a state of *balanced adaptation* to its environment. If removed from such an environment to one in which certain factors are distant from this state of average optimum intensity for all characters, the equilibrium is destroyed and the variety is thrown into a state of *unbalanced adaptation*, in which those characters farthest removed from their respective optima are injuriously affected, while others may be bettered by being placed in a combination of factors of an intensity nearer their optima. A discussion of the practical application of this law and its bearing upon apple culture in the northwest will be deferred for the present and taken up in a later section.

A Comparative Study of the Samples

A close study of the various lots of apples used in this experiment brings to light variations in practically all characters. Many, however, are modifications of charac-

ters inconspicuous in themselves or are slight in amount and so do not attract attention. A complete account of all variations noted would comprise a full technical description of each sample which would far exceed the limits of this paper. For this reason it is thought best to append only some brief comparative notes regarding the more conspicuous variations noted in each variety. In this connection it is well to note the origin so far as known of the varieties included in this study. Arkansas and Arkansas Black, Arkansas; Baldwin, Massachusetts; Ben Davis, probably Kentucky or Tennessee; Delicious, Iowa; Esopus, New York; Gano, probably Kentucky or Missouri; Grimes, West Virginia; Jonathan, New York; Lawver, possibly Kansas; McIntosh, Ontario, Canada; Northern Spy, New York; Rhode Island Greening, Rhode Island; Rome, Ohio; Stayman, Kansas; Tompkins King, New York; Wagener, New York; White Pearmain, probably Eastern States; Willow, Virginia; Winesap, New Jersey; Winter Banana, Indiana; Yellow Bellflower, New Jersey; Yellow Newtown, New York; York Imperial, Pennsylvania. It will be observed that all originated in the east or middle west. Most no doubt appeared as seedlings and were selected and propagated because of their excellence and value when grown under those conditions of environment which prevail at their places of origin; in other words they were individuals which happened to be in a condition of balanced adaptation to that environment. Their behavior under other environments could be determined only by actual tests, and some notes on the subject are included in the following paragraphs.

Arkansas (*Mammoth Black Twig*).—As only one sample of this variety was examined its behavior can be compared only with what is known of the variety in other localities. The fruit was more elongated and conical in shape, smaller in size and less highly colored than that produced in the warmer apple-growing sections of the east. The flesh was inferior in texture, indicating poor development. The variety seems not at all adapted to

the location where grown, but might do better at lower altitudes and in warmer situations in the state. Nevertheless, the quality is not good enough to recommend the variety for dessert, and it is to be hoped that it will not be planted extensively in the northwest. The keeping quality was excellent.

Arkansas Black.—This variety of the Winesap group attains a deeper color than the Winesap and equals that variety in size and quality. The specimens examined were not especially well colored though, it is known to color well in the irrigated valleys. It seems to be better adapted to the conditions of the state than the Arkansas. In keeping quality it was among the best.

Baldwin.—The Baldwin attains its highest perfection in New York and New England, where it is a great favorite in the markets and is produced more largely than any other variety. As grown in this state the fruit is smaller and more elongated than the eastern product and has a more deeply furrowed basin. As grown at Pullman the color lacks intensity, though the fruit is well covered. In the western part of the state the fruit is well colored, especially in the northern part of the Puget Sound Basin. The lots from White Salmon show a good many poorly colored fruits mixed with those of better color, while the quality is rather better than in those examined from other parts of the state. It is, however, inferior to the eastern-grown Baldwin and is evidently poorly adapted to the conditions of the northwest. All of the Washington-grown fruit displayed a tendency to wilt in storage and some of the lots from the western part of the state rotted seriously as a result of fungous infections not apparent on the fruit at the time of storage.

Ben Davis.—Though displaying considerable lack of balance in the adaptation of the different characters to conditions in certain parts of the state, this variety seems on the whole to reach a good degree of development in the warmer valleys. In quality the lot from Missouri was superior to those from any part of Washington, though

many of the Washington-grown apples of the variety were equal to those from most sections of the east. Striking variations in form were displayed by the fruit from different localities. Those lots from the more elevated and cooler sections of the state were of an oblong, conic form and usually had shallow irregular basins, while those from the warm valleys were less elongated and had deep and usually quite regular basins, being more like the fruit from the Ben Davis belt of the east. The fruit developed better texture and quality also in the valleys though it was coarser and more spongy than the eastern fruit. Most of the Washington grown samples of Ben Davis were more decidedly striped than those from the east. This effect is produced by the clearer yellow ground color, which in the eastern-grown fruit is more or less suffused with red. The apples from the elevated localities of Pullman, Cloverland and White Salmon were relatively small in size and poorly colored. Because of its low dessert quality, the planting of this variety for shipment to the east can not be recommended. The most desirable feature of the Ben Davis fruit is its good keeping quality. A tendency to mealiness late in the season was observed in some of the fruit from the irrigated valleys, while those grown at Pullman and Cloverland wilted badly toward the close of the season.

Delicious.—This is one of the newer varieties and when well grown is a dessert apple of fine appearance and high quality. In many of its characters, but especially in flavor and aroma, Delicious resembles the White Pearmain, though in color it bears a likeness to the Winesap group. In moderately elevated situations in some parts of the state it displays a well-balanced adaptation and attains excellent size, color, texture and quality, though none of those examined were quite equal in quality to the Delicious from New York. When grown in too low and warm a location the fruit has a tendency to become overripe and when stored tends to soften in the center, after which it loses greatly in quality. The sample from Clarkston had

a beautiful dark red color, while that from Cloverland was dull in color and poor in texture.

Esopus (*Spitzenburg*).—This is almost the only variety which the writer has examined that attains the first rank as a dessert apple in this state. In certain sections it displays a better balance of adaptation so far as flesh characters are concerned than any other variety. The samples obtained from White Salmon and the irrigated valleys were of excellent quality as dessert apples, though of scarcely as good texture as the variety attains in the east. Overgrown apples are especially coarse in texture. West of the Cascades and in the more elevated locations the Esopus does not reach as high quality as elsewhere. This variety is inclined to wilt in storage unless well grown.

Gano.—This is an apple of the Ben Davis type, but of a more uniform red color. Practically all the remarks included under Ben Davis, aside from those dealing with the distribution of color, apply equally well to the Gano. At its best, the Gano is of slightly better quality than the Ben Davis, which fact, together with its more handsome appearance, renders it a more desirable variety to plant, yet neither can be recommended in a section desirous of building up a reputation and market for dessert apples. It is interesting that both the highest color and the best as well as the poorest quality was attained by apples from the east and middle west.

Grimes (*Grimes Golden*).—This variety, like the Ben Davis, displays considerable variation in form, depending on the locality of production. The specimens from the middle west were roundish to decidedly oblate, while those grown in Washington were all more or less elongated. Those grown west of the Cascades displayed a greater tendency to a conical shape than those from the eastern part of the state, and were also poorer in quality. When grown in the more elevated sections, as at Pullman, Grimes appears poorly developed and immature and is inferior in size and quality. Those from Grandview displayed the best balance of characters and it seems prob-

able that this variety is better adapted to the irrigated valleys than to other sections of the state. All samples were more or less wilted by midwinter, except the fruit from Grandview, which remained firm but showed some tendency to rot. Scald was very bad in the latter part of the season.

Jonathan.—Although rather extensively grown in a number of localities in Washington, none of the fruit which the writer has examined gave evidence of a well-balanced adaptation to the conditions of growth which prevail in the state. All were inferior in color to the fruit obtained from the east and middle west. The apples from Clarkston and the Yakima Valley were of good size but lacked both richness of flavor and aroma. The same lack was evident in the fruit from the western part of the state. At Pullman a pretty good quality is attained, but the fruit does not come up to the requirements as to size and gives other evidence of imperfect development. At Cloverland and in other elevated locations fruit of a poor texture and deficient coloring is produced. Jonathan seems to reach its highest development in certain sections tributary to the Ohio valley and the Washington-grown Jonathans can not compete with fruit from that section when well grown. The samples from Morgantown, West Virginia, were of a beautiful clear dark red color, good size, fine tender flesh, and very high quality. In storage these specimens remained firm and retained their flavor until April. The others wilted considerably after midwinter.

Lawver.—This variety attains good size and fine color in the irrigated valleys, but the quality is not good enough to recommend it to the fruit growers of the northwest. The variety ordinarily keeps well but the specimens stored proved to have poor keeping quality—owing to fungous infection.

McIntosh.—The McIntosh is deserving of attention as a variety of high quality which appears to have a fairly well-balanced adaptation to certain sections of the north-

west. At Pullman the elevation is too great for the best development of the variety, but the Spokane Valley produces McIntoshes of a high degree of excellence. There is good reason to believe that the valley of the northern and northeastern sections of the state can rival the Bitter Root valley of Montana in the production of this variety. The fruit stored wilted badly by midwinter and lost much of its flavor soon after.

Northern Spy.—Of all the varieties examined the Northern Spy seems least adapted to the conditions of growth in this state. As produced in New York and New England this fruit is a dessert apple of the highest quality when well grown and properly colored. In Washington east of the Cascades the color fails to develop and the quality is much inferior to that of the eastern-grown fruit. In the western part of the state the color develops as well as in the eastern states, but the quality is no better than elsewhere in the state. The unsurpassed cooking quality of this variety seems to be largely retained, however, which is its only redeeming feature. It may be worth planting to a limited extent as a culinary fruit for home use, but can not compete in the markets with the eastern-grown Northern Spys. The specimens from the western part of the state were largely infected with fungi, resulting in much decay early in the season. Those from Pullman and Clarkston kept fairly well, though the former wilted badly late in the season.

Rhode Island Greening.—This variety, together with Baldwin and Northern Spy, constitutes the most prominent and successful apples in the orchards of New York and New England. They are also among the varieties least adapted to the conditions found in this state. Their perfect balance of adaptation to eastern conditions is probably to a large degree responsible for their popularity in the east and may also account for the lack of balance which they display in the northwest. As grown at White Salmon and at Pullman the Greening reached a good size, but was decidedly inferior in quality to the specimens

from New Hampshire. At Pullman the fruit was rather flat and strongly ribbed, while at White Salmon the apples were oblong in shape and had, as a rule, rather small cavities. It can not be recommended for Washington, except possibly for local use as a culinary fruit. This variety is a fairly good keeper. Those grown at Pullman wilted badly late in the season, while the lot from White Salmon gave evidence of considerable fungus infection.

Rome (*Rome Beauty*).—This is one of the most popular varieties grown in the state east of the Cascade Mountains and is about the only commercial variety which reaches good marketable size in the high uplands of the Inland Empire. The Rome reaches its highest development in the Jonathan belt of the middle west. The best specimens examined, all characters considered, came from Morgantown, West Virginia. They were of a nearly uniform deep red color, of good size and attractive form, and of pretty good quality for the variety. In many parts of Washington the Rome fails to color well. The specimens from White Salmon and Grandview were especially poor in color. The latter were overgrown and of poor quality, while the former were among the best of the variety. The usual form of the variety is round or nearly so, varying to somewhat roundish conic or roundish ovate. The form of the cavity is subject to quite a little variation. As produced at Pullman and other elevated sections of the state the cavity is very shallow, but becomes deeper in the valleys. The specimens from West Virginia had fairly deep cavities. Indeed it seems probable that those localities which produce Ben Davis of the elongated type also produce Romes with the shallow cavities. The Rome is by nature a culinary apple. In quality it is but little better than Ben Davis. It seems unfortunate, therefore, for the lasting reputation of the industry, that it should have become so firmly established in northwestern horticulture. It is to be earnestly hoped that it may in time be replaced by a variety of better quality. In its adaptations to the conditions of the state, the Rome seems to be fairly well

balanced in most of its characters. The balance, however, is not the same in all sections and is nowhere quite so perfect as in certain localities in the middle states. Most samples kept well until the latter part of the season and then became mealy. The overgrown specimens from Grandview were the first to break down in this way. Those grown at a greater elevation showed a slight tendency to wilt late in the season. None of the samples displayed an inclination to rot until late in the season.

Stayman Winesap.—In both size and quality the Stayman is the best of the Winesap group. Its most serious fault is a rather dull color which often fails to cover the fruit well. The samples obtained from the middle west were of better color and texture than those grown in Washington, though the lot from Indiana were very coarse in texture. Those grown at Pullman were small and inferior in every way. The fruit from Grandview was especially large, flat, and fairly well colored, while that from White Salmon was more elongated, slightly less colored, and rather more aromatic in flavor. These two lots retained their firmness in storage much longer than the others and those from White Salmon scalded badly late in the season. It is very similar to the Winesap in its adaptations.

Tompkins King.—This variety is popular in the western part of the state, where it attains a large size and good color, though the latter character develops well at Pullman. None of the samples equaled in quality the variety as grown in New York. Those grown at Pullman had a very good flavor, though the flesh characters were those of poorly matured fruit. The fruit from the western part of the state was of a fairly elongated conic form, while that grown at Pullman was shorter and strongly ribbed. This variety appears to be but poorly adapted to Washington conditions. The fruit grown at Pullman wilted badly late in the season, while that from western Washington rotted considerably owing to fungus infections.

Wagener.—Though of the Northern Spy class, the

Wagener displays a much better balance of adaptation to the conditions of the state than the Northern Spy. It seems to reach its best development in the cooler regions of the state. The specimens from Grandview were of good size and very juicy, but were poor in color, coarse in texture, and deficient in flavor. Wagener develops especially well in the Spokane Valley. The specimens from Opportunity were large, well colored, and of excellent quality, though somewhat coarse in texture. Those grown at Pullman were more aromatic but possibly not so rich in flavor and did not develop sufficient size. This variety does well west of the Cascades and especially in the northern part of the Puget Sound Basin. The specimens from Eastsound were large, highly colored, and fine in texture, but less aromatic than the eastern Washington fruit. The samples obtained from West Virginia gave evidence of having been grown too far south. They were poorly colored and of rather poor texture, but of good size and excellent flavor. In form the fruit from Opportunity was roundish, that from Eastsound roundish conic, while the remainder was decidedly flattened and all samples were more or less strongly ribbed. This variety shows very little tendency to wilt in storage. The fruit from the highlands keeps well, but that from the irrigated valleys shows a tendency to physiological decay. Scald is serious after midwinter.

White Pearmain (*White Winter Pearmain*).—In general appearance this variety often closely resembles the Yellow Newtown, but is usually more elongated and more largely blushed. Moreover, it is quite different in flavor and is remarkable for its fine aroma. It is a variety of high quality and attractive for a yellow apple, moreover, it attains its good qualities in the irrigated valleys better than on the highlands, the specimens from Cloverland being dull and green in color and poor in texture, but well blushed and highly aromatic. Its worst fault is susceptibility to the apple scab. It would seem to be better adapted to growing in the state than some of the more

popular varieties. The fruit from the Yakima Valley retained its firmness much better than that from Cloverland, but lost somewhat in flavor toward the close of the season.

Willow (*Willow Twig*).—The writer has examined this variety only as grown in the elevated portions of eastern Washington. In such locations it does not develop especially well in either size or color and is of too poor quality to be worthy of consideration. Moreover, it wilts badly in storage, though when well grown the fruit has excellent keeping quality. It is evidently poorly adapted to this section.

Winesap.—In some of the irrigated valleys this variety is one of the most popular apples grown. It attains a good marketable size and an attractive color, though none of the samples examined were equal in color or quality to the Winesaps from Indiana and West Virginia. In elevated localities, as at Pullman, Cloverland and White Salmon, the fruit is small and poorly colored and has flesh characters indicating imperfect development and maturity. As grown in the irrigated valleys the fruit is apt to be deficient in flavor, and, if large, coarse in texture. The lot from Cashmere showed the best balance of characters of any Washington, grown specimens, but these were in no way superior to the Winesaps from West Virginia. It is probable that the better grown fruit from the eastern Winesap districts is equal to that grown in Washington in all respects, with the possible exception of size, which, if large, is, as noted, apt to be accompanied by deterioration in quality. It is evident then, that the balance of adaptation of this variety to northwestern conditions is imperfect at best and that the planting of Winesaps in Washington may easily be overdone. This variety proved to be one of the best in keeping quality. Those from Pullman and Cloverland wilted late in the season, though most of the other lots were in excellent condition in April and a few were held in storage until July.

Winter Banana.—As only a single lot of this variety

was examined in detail, it is difficult to make very positive statements regarding its behavior in the state. Though less desirable than a red apple, it is a variety of handsome appearance and is fairly good in quality. It is perhaps rather better adapted than the average to certain sections of the state and appears to develop best in fairly elevated situations. It is especially well liked in the Spokane Valley, and fruit grown there is said to have good keeping quality, though the specimens from western Washington were past season by midwinter. They wilted badly and showed much scald.

Yellow Bellflower.—This variety appears to be better adapted to the western part of the state than to the irrigated valleys. The apples from Clarkston were coarser in texture, milder in flavor and poorer in quality than the samples received from the east. There were no very striking differences in form, structure or appearance except that the eastern Bellflowers were more often blushed than those from Clarkston. The apples from Puyallup were overgrown specimens from young trees, were coarse and spongy in texture, and inferior in quality. As this is a tender fruit, easily injured by careless handling, and does not appear to be especially well balanced in its adaptations, it is not desirable to plant extensively for shipping. Moreover, it is not a good keeper. The specimens from Puyallup were practically past season when received and those obtained from the east were more or less injured and such specimens decayed quickly. Some of the lot from Clarkston, however, kept sound and firm until past midwinter, but deteriorated in flavor toward the last.

Yellow Newtown.—When at its best, this variety has few equals. It is narrow in the limits of its adaptations and its successful culture in the eastern states is confined to small areas, where, however, it is in nearly perfect equilibrium with its environment. In many places in the northwest it is grown successfully, though it scarcely equals in quality the best eastern product. The fruit from White Salmon and some of the irrigated districts

was of excellent quality, but coarser and less delicate in texture and of not quite so good flavor as the apples from West Virginia. The specimens from Cloverland were hard and green and gave evidence of imperfect maturity. Evidently the elevation is too great for its proper development. The single sample from western Washington consisted of well-colored, extensively blushed fruit, but was inferior in quality. Owing to its limited area of successful production in the east, it is worth planting in Washington wherever its characters give evidence of a fair degree of balance of adaptation with the environment. This variety is perhaps a better keeper than Winesap. Some of the fruit from White Salmon kept in good condition until July, though overgrown fruit and that which has been exposed to heat before storage showed signs of physiological decay late in the season. Underdeveloped specimens wilted in storage.

York Imperial.—In sections of Virginia and neighboring states the York Imperial occupies the place of supremacy held by the Baldwin farther north. This is doubtless due to its perfect balance with the environmental conditions of that region, and, like the Baldwin and other sorts perfectly adapted to their eastern habitat, this variety finds itself out of equilibrium when moved to the northwest. The apples from western Washington were of good size and color, but were coarse and undesirable in texture and poor in quality. The specimens grown at Pullman were smaller, more elongated, and less compressed than the others, and the axes were less oblique. They were somewhat better in quality, though not good enough to justify more extensive planting. The fruit wilted in storage, and that from western Washington gave evidence of fungous infection and scalded badly after midwinter.

Discussion of the Effect of Environment Upon Apple Characters

Size.—Size is the direct result of development. An apple will reach its maximum in growth when all factors

are at the variety optimum for the physiological processes upon which development depends. A departure from this optimum, whether toward a greater or less intensity, means a decrease in size, as is observed in approaching either the northern or southern range of a variety. It has been frequently noted, however, that the optimum for growth is not the best combination of factors for the development of certain other desirable characters, so that it is well to choose an environment having certain factors in a somewhat less degree of intensity, being content with fruit of fair size but superior in other respects. Since the apple contains about 85 per cent. of moisture it is evident that the water supply is a factor of prime importance in determining size. It is possible by excessive irrigation to force an abnormal growth of the fruit, though always apparently at the expense of texture, flavor, and keeping quality. It is evident, then, that if fruit of good quality is expected, irrigation must be moderate in amount, especially with vigorous young trees. Thinning may result in increased size owing to the larger amount of moisture available for each fruit. Temperature and length of season are of importance in determining, respectively, the rapidity of growth and degree of development attained.

Form.—One of the striking features revealed by the study of a number of varieties from several localities is the fact that the modification in shape due to the difference in environment is by no means uniform for the several varieties. Some varieties are quite constant in shape while others are much more plastic in this respect. Moreover, certain varieties are much more easily influenced than others which respond in the same way, while still others respond differently to the same factors. One of the most frequently observed and conspicuous modifications of form consists of the elongation of the axis of the fruit relative to the horizontal diameter. This character has been especially studied, in the case of the Ben Davis, by Shaw, who found the elongation most noticeable in fruit from the northeastern states, the mari-

time provinces of Canada, and the Pacific coast. Shaw's papers dealing with this subject have already been noted. Upon studying the climate in these localities, it was found that the temperature for two or three weeks after the blooming season was notably lower than in the sections where the Ben Davis assumes its normal shape. Since this appeared to be the only factor constant for the several localities, it is suggested as the explanation of this variation. It has been shown, however, that temperature is incapable of influencing form except by its action through the functions of the plant in modifying the effect of some other factor. It is the writer's opinion that the elongation is due to the relative moisture supply of the different parts of the apple at this period of development as influenced by the temperature; that it is primarily a modification due to the moisture relation rather than to the direct effect of temperature, the latter being a secondary cause. The rapidity of circulation of the sap and therefore the supply of moisture to the organs of the plant is greatly influenced by the temperature. It is a well-known fact of plant physiology that much less moisture passes through the plant in the cool days of spring than during the warmer weather of midsummer. A reduction of the temperature at this time results in a still more sluggish movement of the sap. In the period immediately after blooming the energy of the plant, so far as the development of the fruit is concerned, is directed primarily to the proper nourishment of the growing seeds and the adjacent parts. If at this time the circulation of the sap is retarded by a temperature unwontedly low for the variety, the moisture supply of the fruit is lessened and a relatively larger amount goes to the seeds and adjacent parts, while the pulpy portion of the fruit receives a more scant supply. As a result, the axillary development is proportionately greater than the swelling of the fruit due to the accumulation of moisture in the superficial tissues. After some two or three weeks the form of the fruit becomes fixed and is not noticably influenced by the moisture supply thereafter.

The elongation of the fruit is usually accompanied by a constriction of the apex resulting in a conical form. This may be due to the greater development of the basal portion, which is adjacent to the point where the sap enters the fruit and may therefore be better supplied, though the physiology of fruit development is in need of further study. In the Grimes, however, an oblong form results. The McIntosh, as grown at Pullman, is often decidedly obovate, a variation which the writer ascribes to the same influences that produce the elongated conic form of the Ben Davis and other varieties, though in this variety the response is somewhat different. The Rhode Island Greening, Willow and Wagener, as a rule, fail to assume an elongated form in localities where it is well marked in some other varieties. Also in certain varieties which are naturally conic in form and considerably elongated, as Delicious and Yellow Bellflower, this effect is not evident. The larger number of varieties, when grown in this state, have a more ribbed form than the same varieties in the east. This seems to be due to a lack of balance in adaptation, though the particular factor which gives rise to the variation has not been determined. Some varieties, like the York Imperial and the Yellow Newtown, are compressed in form, that is elliptical in section, and have an oblique axis when grown in certain environments. These characters seem to be in some way related to the better development of the fruit, as they are less evident in fruit from the elevated and unfavorable sections of the state. Beach has noted in the "Apples of New York" a similar difference between the Newtowns of western New York and those of the Hudson Valley, the latter having a more oblique axis and elliptical form.

Stem.—The stem is one of the most variable structures of the apple, and, owing to the fact that stems of different lengths, diameters and shapes are commonly found in any lot of apples grown under practically uniform conditions, it is difficult to associate such variations with the environment. The writer has noted, however, in the case of some short-stemmed varieties, like the York Imperial,

that those lots grown under less favorable conditions had, on the average, longer stems than others grown under a more favorable environment.

Cavity.—The most conspicuous variation in the cavity is in its depth. This is of especial note in the Rome, which has a very shallow cavity in most parts of the state. This is doubtless due to the same cause which produces the elongated form of the fruit in many varieties, namely the elongation of the axis resulting from a deficient moisture supply incident to a low temperature after the blooming season. In this variety the elongated axis obliterates the cavity instead of modifying the general outline of the fruit. The same variation is also noted to a less degree in a number of other varieties. An especially furrowed cavity is often observed associated as a rule with the ribbed form of fruit.

Calyx.—The writer has failed to observe any modifications of importance in the calyx lobes of the fruit. The size of the calyx cup or "eye" of the apple is influenced by the development of the fruit. In large fruit this opening is apt to be large, so that the lobes are separated, resulting in an open or partly open calyx. Small or poorly developed apples, on the other hand, usually have the calyx closed.

Basin.—The depth of the basin seems to depend upon the same factors as that of the cavity and seems to be much more readily influenced than the latter. The width is often associated with the form of the apple, a very constricted apex resulting in a narrow basin. A much furrowed basin results from a combination of factors unfavorable to the best development of the fruit.

Skin.—Statements have often appeared in regard to the effect of various climatic factors upon the thickness and toughness of the skin. Estimates of these characters, however, appear to be based entirely upon sense impressions of the observers, although it would seem that exact measurements would not be especially difficult. In the absence of such accurate data, an expression of opinion

would be premature. Dry air and sunshine are favorable to the production of clear, smooth skin.

Color.—There seems to be no doubt that the coloration of apples depends upon the influence of several factors of which light is usually the most important. The importance of light is easily demonstrated by covering the fruit during development either wholly or in part. The intensity of illumination is also, evidently, quite narrow in its limits, so that a point is soon reached at which the color begins to pale owing to excess of illumination. It has been frequently noted that apples grown near the southern limit of the range of a variety are paler than those grown farther to the north. This effect appears to be the result of an excess of the two factors, heat and light. It has been mentioned in the discussion of the characters of several varieties that, contrary to the general impression, those grown in Washington east of the Cascades where insolation is intense were less highly colored than those from western Washington or the eastern states. The most marked example of this kind which the writer has observed is the Northern Spy. Again, contrary to the general impression, most of the samples from elevated locations were poorly colored, a fact which may be attributed partly to the strong insolation and partly to the poor development due to the low summer temperature. It appears, therefore, that either too strong or too weak illumination may result in poorly colored fruit and that the best color is developed under a condition of optimum intensity of the light.

It is suggested above that temperature may influence color. This is most commonly observed in the case of apples grown under conditions of too high summer temperature, though a deterioration in color also results if the temperature is much below the optimum for the variety. It is often stated that apples become more highly colored the farther north they are grown. This is only true in part. Those varieties which are adapted to the most northerly portions of the apple belt are able to develop their highest

color at the limit of winter hardiness of the tree. The southern varieties, on the other hand, require for the best development of color a higher summer temperature than is experienced in the northern localities. The Winesap, for example, when grown in Central New York is partly covered with a pale red. At Pullman the majority of varieties color poorly, due at least in part to the cool climate. That the temperature and not the shortness of the season is the factor involved is shown by the fact that most of these varieties color well in central New York which has a season of about the same length though averaging several degrees warmer.

Cultural conditions may influence the color to a certain degree. In general those processes of orchard management which favor the early maturity of the fruit result in improved color, especially in localities having a short growing season. Pruning and wide planting are regarded as favoring high coloration by admitting light into the tree, though it is possible that in regions where the light is intense these factors may not be of so great importance in their effect upon color as in less sunny locations. Something has been said of the influence of the soil in the discussion of the literature and it has been noted also that studies of the effect of fertilizers upon the color have not yielded satisfactory or uniform results. The influence of iron compounds is worthy of brief discussion in this connection. It seems evident, from the chemical studies which have been made, that the red pigment includes iron in its composition. This has sometimes been assumed to mean that the chief requirement for highly colored fruit is the presence of plenty of available iron compounds in the soil. As a matter of fact, iron is also necessary to the formation of chlorophyll and most soils contain an abundance of that element for the purpose. From the chemical data compiled by Stewart[5] it appears that the ash of the fruit contains a much smaller proportion of iron than that of the leaves. It is logical to conclude, therefore, that soils containing suffi-

[5] Pa. Sta. Rept. for 1910–11.

cient iron for the development of chlorophyll in the leaves are also fully supplied for the formation of the red pigment of the apple.

Internal Structure.—The form and relative development of the core and associated structures are subject to numerous variations, which, however, are seldom so conspicuous as to attract attention unless closely studied, and appear to be of little practical importance to either the grower or consumer of the fruit. The number of seeds may be mentioned as an indication of the thoroughness of cross pollination and in most varieties the presence of one or more well developed seeds is a requisite to the proper development of the fruit. Small or poorly developed fruit, the result of too short a season or too low a temperature, is apt to have the core closed and axile, or nearly so, while in the same varieties good development is usually associated with a more open abaxile core. The carpels of such poorly developed fruit are usually entire and smooth, while those of the better-grown fruit are more or less cleft and often tufted.

Flesh Characters.—From the standpoint of the consumer, these are by all odds the most important characters of the fruit, though lost sight of through the emphasis placed on external characters, and no grower who has at heart the permanent prosperity, extension and normal development of the industry can afford to look upon quality as a secondary consideration. Neglect in this matter is sure to result sooner or later in a bad reputation for the fruit among a considerable proportion of buyers, which appearance and advertising will not be competent to overcome. The fact can not be denied that the great majority of varieties fail to attain as high quality in the northwest as when grown in the eastern or middle states where nearly all of them originated, while at the same time they may excel in other important characters. This is especially true of most of the choice dessert apples. Such unequal development can have no other interpretation than that these varieties are in a state of unbalanced adaptation to the environment. This

fact being recognized, the main question is, How can this disadvantage be overcome? Evidently the solution does not consist in a steadfast refusal to face the situation and vehement declaration that the fruit of any particular district is the best that can be produced. Such tactics, though well meant, can be permanently successful only when the statements are justified by the facts. If apple culture in Washington is to be maintained upon a sound basis it will be necessary first of all that growers shall exercise great care in planting to choose those varieties most nearly in equilibrium with the environment in the various sections of the state, at the same time avoiding over-irrigation or other errors in orchard management which may tend to an unequal development of the characters of the fruit, usually at the expense of quality. Even this, however, may be but a temporary makeshift, since few if any of the better varieties possess the requisite power of adaptation. It will be necessary first of all to determine if the variations which appear when apples are grown from seed in the northwest are more favorable in character than those which are displayed by introduced varieties. If such should prove to be the case the writer is under the conviction that the apple culture of the northwest should ultimately be largely made over on a basis of new varieties of local origin. A number of such varieties have already appeared, but unfortunately some of them have been chosen with little regard for quality. No work of greater value to the future horticulture of the region can be undertaken by the experiment stations of the northwestern states than the development of apple varieties of high quality and perfect adaptation to the various sections of their respective states.

The apples of high quality which show a fair degree of adaptation to the irrigated sections are Esopus, Yellow Newtown, Delicious and White Pearmain. The last was found by Lewis, of the Oregon station, to be one of the best pollenizers on every variety tested. Jonathan, Winesap and Stayman, though largely grown, shows in general a poorer balance of characters. In the more

elevated valleys Wagener, Delicious and McIntosh are doubtless most worthy of culture. The highlands of eastern Washington are very poorly adapted to the growing of winter apples, though some of the early apples do fairly well, among which may be mentioned Oldenburg, Gravenstein and Yellow Transparent. On account of the abundance of sunshine the Oldenburg develops a high sugar content for the variety which counteracts its natural acidity and results in an apple of pretty good dessert quality. Of the winter apples, Rome reaches good marketable size but the quality is not high and the eastern market should not be jeopardized by shipping this variety. The Palouse, an apple of local origin, is of much better quality, but has little standing in the market as yet. The Dutch Migonne, a variety from western Europe, shows a better balance of characters in eastern Washington than in most other sections of this country. It is of good size, fairly well colored and excellent in quality.

Many varieties popular in the eastern states color better west of the Cascades than in eastern Washington, though there is usually manifest a lack of balance in other characters. In certain respects the environment resembles that of western Europe and many of the varieties of cherries, plums, prunes, and other fruits of that country do very well here and, indeed, in other sections of the state as well, though in a number of instances varieties of northwestern origin are gaining in favor rapidly. Apple breeding, however, requires more time for its accomplishment and further importations of fruits, especially apples, adapted to the mild climate of western Europe would no doubt prove an advantage through the possible discovery of sorts adapted especially to the western part of the state.

Quality is not in itself a simple character. It depends upon all the characters of the flesh which determine the desirability of the fruit for eating, such as texture, juiciness, aroma and flavor. Fineness of texture evidently depends upon a proper combination of favorable factors.

Conditions favoring rank growth result in coarse texture, as was observed in several instances in the case of apples grown under irrigation, especially if the fruit was overgrown. Some of the fruit from young trees also was overgrown and coarse. Tenderness depends upon the development. Poorly grown, under-developed fruit grown where the temperature is too low or the season too short for the variety has hard flesh which becomes spongy rather than mellow toward the end of the storage season. Overgrown fruit of certain varieties, on the other hand, often shows lack of coherence between the cells, often accompanied apparently by larger intercellular spaces, and such fruit tends to become mealy as the season progresses. Juiciness is primarily a manifestation of the amount of moisture in the fruit, but is also associated with the tenderness of the cell walls and their tendency to break rather than to separate. In general an abundance of moisture results in juicy fruit though the juiciness is not in proportion to the moisture supply. The substances which give the apple its aroma are present in such small amounts that their investigation is difficult. They are volatile compounds and affect the flavor of the apple largely by their action on the sense of smell. A cool climate is favorable to their production and it was often observed that they were most strongly developed in the apples from elevated situations. Flavor depends upon the kinds, amounts and relative proportions of the soluble solids, especially the balance between sugars and acids, and will be given further consideration in the discussion of the chemical composition. Immature and under-developed apples contain some tannic acid, which is often sufficient in amount to give an astringent character to the fruit.

Keeping Quality.—In its relation to the environment, keeping quality evidently follows the same rule as other variable characters of the apple, namely, that for any variety the keeping quality depends upon the optimum intensity of the various external factors. Apples grown where the temperature is too low or the season too short

to develop the fruit to a proper stage to keep well, soon wilt, lose flavor and scald, or show other evidence of deterioration as was frequently observed in the fruit from high altitudes. On the other hand, too great excess of certain factors results in overgrown or overripe fruit having a tendency to rot, mealiness, or physiological decay, as in the case of the Yellow Bellflowers from Puyallup and some of the fruit from the warm valleys. The balance of factors favorable to good keeping quality does not appear to differ much from that which produces the fruit which is most desirable in other characters, though it is possible that the required intensity of some factors may be slightly lower. It appears, therefore, that a good balance of the other characters of the fruit and perfect adaptation to the environment will be accompanied, as a rule, by good keeping quality, provided that the fruit is properly handled and not infected with disease, while an unbalanced adaptation of characters to environment is likely to result in poor keeping quality. It seems probable that irrigation in itself does not result in poor keeping except when improperly applied or carried to excess or associated with other factors in such a way as to destroy the equilibrium of the environment. The relation of specific gravity to the keeping quality is discussed in a succeeding paragraph.

Specific Gravity.—It has long been understood that varieties of apples differ in their relative weights; thus Wolf River is comparatively light and Baldwin is generally regarded as a heavy apple. The only record found of the determination of specific gravity of apples is that of Howard's work in the National Bureau of Chemistry, Bulletin 94, in which it is noted that the specific gravity diminished 3 per cent. to 5 per cent. during storage. From the account it is not clear whether the determinations at the different dates were made with the same apples. The decrease of specific gravity is ascribed to the increase of air spaces between the cells due to the softening of the middle lamella. In the specific gravity determinations made by the writer a number of points was noted.

The different lots of a variety may differ considerably in specific gravity, though as a rule running somewhat close together, thus Ben Davis and Gano are apples of low specific gravity, while Grimes, Stayman, Wagener, and Yellow Newtown run rather high and Baldwin and Rome may be classed as medium in this respect. Overgrown apples were low in specific gravity, probably owing to more air space between the cells. This is more apparent upon examining the results for individual apples than upon comparing the average for different lots, as in the latter case the extremes are modified by averaging with the results for more normal specimens. On the other hand, small and rather undeveloped apples are apt to have a high specific gravity on account of their solid flesh and usually closed core. Juicy apples, if not overgrown, have a high specific gravity when the juiciness is due to a high moisture content.

The relation of specific gravity to keeping quality is of interest. While some late keeping varieties have normally a low specific gravity, those lots of a given variety having a high specific gravity for the variety are usually the best keepers. This is in line with the fact that certain causes which give rise to fruit of poor keeping quality also produce a low specific gravity. This is shown very strikingly by a comparison of the specific gravities as calculated month by month through the season. As the calculations were made at the time the fruit was found fit for use, the monthly averages show the steady increase in specific gravity with the better keeping quality of the fruit, though modified somewhat by the peculiarities of the different varieties which happened to be in season at different times. These averages are as follows: November and December, 0.787; January, 0.787; February, 0.810; March, 0.831; April, 0.852. Though these results may seem to be at variance with Howard's observations it is possible that if the same specimens had been tested at intervals a decrease in specific gravity would have been noted.

Chemical Composition.—In order to throw some light,

if possible, upon the relation of chemical composition to the other characters of the apple and to determine whether the composition is influenced by the environment, the juice of the various samples of Grimes, Jonathan, Winesap and Yellow Bellflower was analyzed by the department of chemistry.

The juice of the Grimes and Winesap contains, as a rule, a decidedly higher percentage of total solids than that of the Jonathan and Yellow Bellflower. It is also generally higher in specific gravity and has a greater viscosity. In Grimes and Yellow Bellflower the juice of the eastern-grown fruit contains a large proportion of total solids than that of the Washington grown fruit, though this rule does not hold good in the other varieties. The apples from the irrigated valleys and western Washington were low in total solids with the single exception of the Winesaps from Cashmere. The analyses fail to show any constant difference in sugar content in favor of the fruit produced in the sunny climate with long hours of daylight characteristic of the apple-growing sections of the state.

In Grimes the total sugars are fairly high and the proportion of sucrose is especially large. The acid content, on the other hand, is low as a rule. The result is a rich, mild or nearly sweet flavor. A sample from Puyallup showed the lowest sucrose content combined with the highest acid content, and this was the least rich as well as the most acid in flavor.

Jonathan, on the other hand, displays a low content of total sugars and especially sucrose, while the acid content is slightly higher than in Grimes, indicating a subacid apple, lacking in richness. The lots from Missouri and Indiana were highest in sucrose but were of scarcely as good quality as the Jonathans from West Virginia. The latter were low in both sucrose and acid, but displayed a good balance between these constituents, indicating an apple with rather thin juice, not very rich, but pleasant and refreshing. Its evident superiority resulted largely

from the fine texture and well-developed flavoring constituents not shown by the analysis.

The Winesaps, though high in total sugars, are low in sucrose, indicating a heavy juice rather lacking in richness. The comparatively high acid content corresponds to the sprightly subacid character of the fruit. The highest acid content was found in the fruit from Cloverland, where it is associated with a total lack of sucrose resulting in a comparatively poor fruit. The apples from Cashmere and White Salmon were also devoid of sucrose in the juice, but the acid content was low and the flavoring principles well developed, as a result of which the quality was fairly good. The poorly developed Winesaps grown at Pullman were deficient in sucrose, acid, and flavors and were correspondingly poor in quality.

The Yellow Bellflowers, though low in total sugars, were rather high in sucrose and also in acid. The balance between these constituents is good and results in a moderately rich, pleasant, subacid flavor.

Summary

The opportunity for the study of apple variation was unusually good, owing to the facilities afforded for the examination of fruit from various localities and different environments, and it has been possible to work out the fundamental principle upon which variation resulting from external factors depends and to apply it in the study of environmental adaptations. This principle, the *Law of the Optimum,* states that, for any given variety there is for each character a certain intensity of each essential factor of the environment at which, other conditions remaining the same, that character reaches its highest development.

In the application of this law to varietal adaptations, the essential point is the proper balance between characters and environmental factors, that is, all factors should be of such an intensity as to permit a good all-round development of the fruit. In the absence of such

a balance certain characters may fail to reach a proper degree of development while others develop to excess.

The failure in quality and other respects of many of the best dessert varieties of apples when grown in Washington is due to such a lack of balance. Practically all of them originated under a much different environment and were selected and came into prominence owing to their perfect balance of adaptation in localities having a set of external conditions similar to those under which they originated. The hope of northwestern apple culture in the future lies in the careful selection of varieties and the origination locally of varieties of high quality showing adaptation to the conditions of growth in the various sections. In the meantime plantings should be made from those varieties of high quality which show the best adaptation. These are Esopus, Yellow Newtown, White Pearmain and Delicious for the irrigated valleys, and Wagener, Delicious and McIntosh for the higher valleys of northern and eastern Washington. Jonathan, Stayman and Winesap show a poorer balance and should not be planted too recklessly. The climate of the Pacific coast resembles that of western Europe more than that of the eastern states, and further importations of European varieties is desirable especially for testing west of the Cascades.

The moisture relation is probably the most important factor in inducing variations, and is doubtless responsible for certain variations which have been ascribed to other causes which act indirectly by modifying the moisture supply. The elongation of the fruit following a cool period after blooming may result from a diminished circulation of the sap, giving rise to an insufficient supply to provide for the simultaneous development of the fleshy portion and elongation of the axis. Variation in the depth of the cavity and basin in certain varieties is probably to be explained in a similar way.

Color modifications depend to a great extent upon the light relation and somewhat upon development as influenced by temperature. The optimum intensity for the

production of red pigment is quite narrow in most varieties and poor color may result from either deficiency or excess. Latitude and altitude affect the color only as they modify the factors upon which color depends, causing them to approach or recede from the optimum. The influence of elements in the soil is not well understood. It is probable that soils containing sufficient iron for the proper development of chlorophyll contain an abundance for the production of red pigment in apples.

Aside from such differences as depend upon the handling of the fruit, variations in keeping quality appear to follow the law of the optimum in the same manner as the other characters of the fruit. Conditions which favor the best all-round development result, as a rule, in good keeping quality. Apples grown under irrigation are said to keep poorly probably because of their unbalanced adaptation to the environment. Certain factors which favor development and maturity are present in excess, resulting in overgrown or overripe fruit.

Varieties differ in specific gravity according to the extent of intercellular spaces in the flesh and the openness of the core. Overgrown specimens are low in specific gravity. As a rule, those lots which kept best in any variety had the highest specific gravity.

Chemical composition is associated somewhat with quality. High sucrose content results in richness of flavor. Fruit of high quality has the sugars and acids well balanced and the flavoring constituents well developed. A heavy juice is usually associated with a high content of soluble solids. Fruit grown under irrigation is ordinarily rather low in soluble solids. There seems to be no constant relation between the amount of sunlight and the production of sugars, and flavors appear to develop best in a relatively cool climate.

VARIATION AND CORRELATION IN THE MEAN AGE AT MARRIAGE OF MEN AND WOMEN

SOMEWHERE in sociological literature we have met with the statement that whereas the mean age at marriage of men differs from district to district because of social and economic conditions, the mean age at marriage of women varies but little because of these factors. In view of the high "assortative mating" coefficient[1] for age of bride and groom, this statement seemed so remarkable as to be open to question.

Its validity can be very easily tested provided the mean age at marriage of men and women from a series of districts differing in economic and social conditions are available. If the mean age of women is independent of these conditions, or far less dependent upon them than that of men, one should find (i) that the variation of mean age of brides is lower than that of mean age of grooms, and (ii) that for a series of districts the coeffiicent of correlation between the mean age of brides and grooms is very low.

The only suitable series of data that we have been able to find is that given by A. Dumont[2] for the average age in years and months at first marriage of the males and females of the 87 departments of France. Grouping his data in classes of five months' range, we find, in terms of months:[3]

	For Men	For Women
Mean	$337.76 \pm .80$	284.43 ± 1.03
Standard deviation[4]	$11.03 \pm .56$	$14.25 \pm .73$
Coefficient of variation	$3.26 \pm .17$	$5.01 \pm .26$

[1] See Lutz, *Science*, N. S., Vol. 22, pp. 249–250, 1905. For a general review of the literature of assortative mating see Harris, *Pop. Sci. Mo.*, Vol. 80, pp. 476–492, 1912.

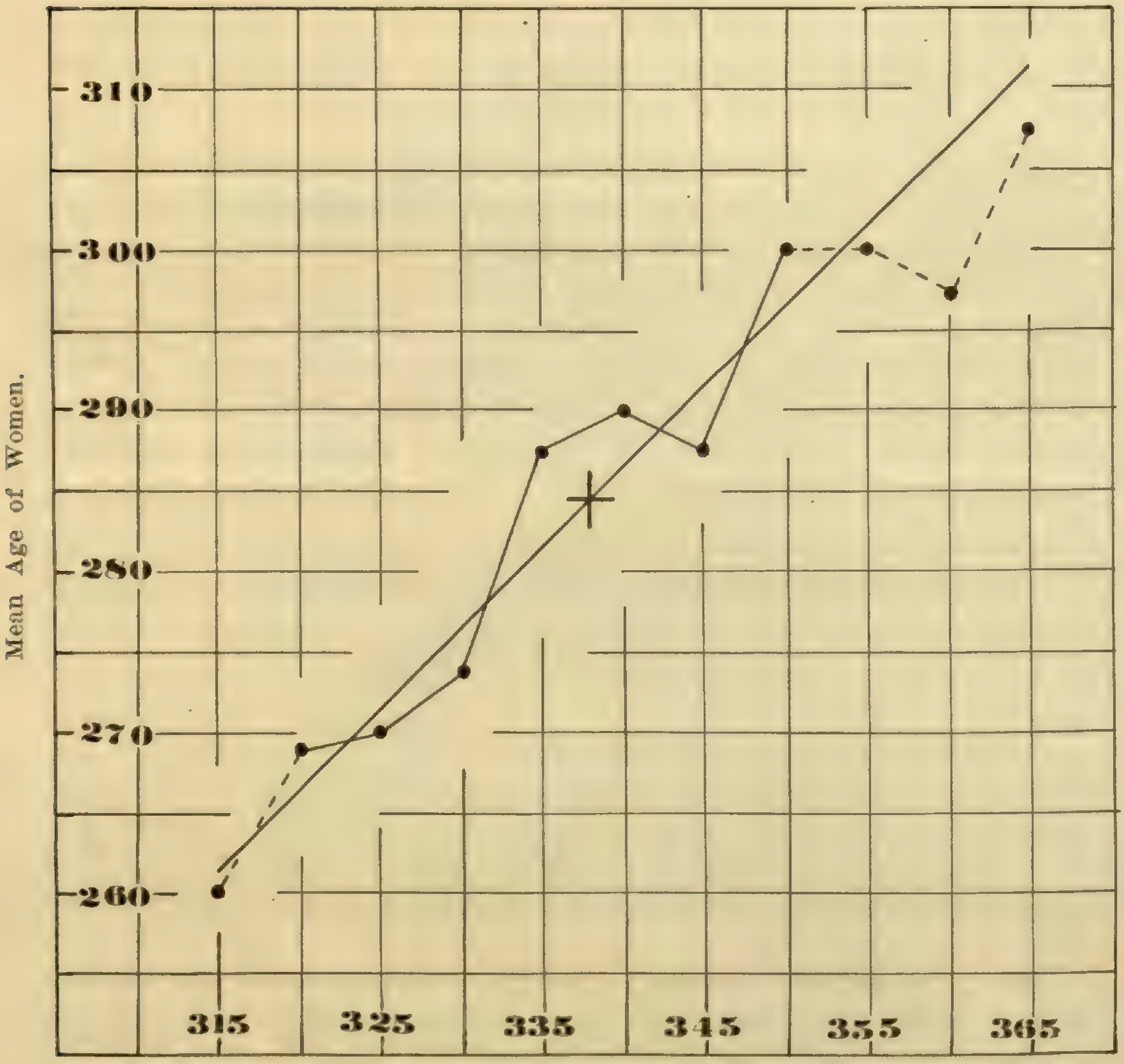
[2] Dumont, A., *Rev. Ecole Anthrop. Paris*, Vol. 14, p. 163, 1904.

[3] The results given by the ungrouped data are:

	For Men	For Women
Mean	$337.87 \pm .83$	284.45 ± 1.01
Standard deviation	$11.49 \pm .59$	$14.00 \pm .72$
Coefficient of variation	$3.40 \pm .17$	$4.92 \pm .25$

Considering the shortness of the series, the results are in as good agreement as could be expected.

[4] Without Sheppard's correction for the second moment.



Mean Age of Men.

We note that the women marry on an average about four years and five months younger than the men. Contrary to what we have been told, their mean age at marriage both absolutely, as measured by the standard deviation, and relatively, as measured by the coefficient of variation is *more* variable than that of men. The difference in standard deviations for the ungrouped material is 2.51 ± .93 and for the grouped records 3.22 ± .92. These are 2.71 and 3.49 times their probable error, and hence perhaps significant. For the coefficient of variation, the differences by the two methods are 1.52 ± .31 and 1.74 ± .31. These are 5.69 and 4.96 times their probable errors and their significance is even more probable than those for the standard deviations.

The correlation coefficient from the grouped data by the product moment method, using the means and standard deviations given above, is

$$r_{mf} = .781 \pm .028.^5$$

Thus on a scale of -1 to $+1$ the interdependence of mean ages of men and women is very close indeed.[6] Expressing the same relationship in terms of regression by the well known formula

$$f = \left(\bar{f} - r\frac{\sigma_f}{\sigma_m}\bar{m}\right) + r\frac{\sigma_f}{\sigma_m}m,$$

where the bars indicate population means and the sigmas population standard deviations of $m =$ males and $f =$ females,

$$f = -56.474 + 1.009\ m.$$

Thus we see that each month's increase in average male age is followed by a month's increase in mean female age. The fit of the straight line to the empirical means as shown in the diagram is excellent—considering the small number of the district means from which the equation is deduced.

Thus the available data show that the mean age at marriage of women instead of being less variable from district to district than that of men is actually more variable—both absolutely and relatively.

In short, there is, as far as our data go, no evidence for the assertion that while the time of marriage of men is closely dependent upon the complex of social and economic conditions that of women is practically independent of them.

We have published this note in the hope that it may suggest to some one with the opportunities of obtaining really adequate data an investigation of the problem which has several rather important points of interest.

J. ARTHUR HARRIS,
ROXANA H. VIVIAN

COLD SPRING HARBOR

[5] The difference method applied to the ungrouped material gives

$$r = .763 \pm .030.$$

The difference is of no significance.

[6] Possibly, however, the relationship is in part spurious. The mean of males and females were taken on the basis of the same N, or approximately the same N, for the various districts. Data for investigating this question are not available. The point should be borne in mind by a subsequent worker.

DUPLICATE GENES

Some interesting questions are raised by a recent article by Gregory: "On the Genetics of Tetraploid Plants in *Primula sinensis*."[1] Reciprocal crosses of two races of *P. sinensis* were made. One cross gave entirely normal results in F_2 as regards chromosome number and hereditary characters. The reciprocal cross gave an F_1 generation which was sterile with the parents and produced only a giant variety in F_2. This proved to have the tetraploid chromosome number. Experiments indicated that the genetic factors had also all been doubled, a very significant parallelism.

Gregory uses the nomenclature AAAA, AAAa, AAaa, Aaaa, and aaaa to represent all the possible conditions as regards a pair of Mendelian factors. He states that heterozygotes of the form AAAa should give gametes AA and Aa, and should produce, on selfing, the zygotes AAAA, 2AAAa and AAaa, and that the last class selfed should produce recessives. On the chromosome theory of heredity, this assumes that the four chromosomes concerned are equally likely to pair in synapsis in any of the possible ways, a very interesting phenomenon if the assumption proves correct. But it is conceivable that two independent synaptic pairs may be formed. It may be that only chromosomes from the same original race pair in synapsis. It is true that the first of the original crosses shows that the chromosomes of the two races can enter into normal mitosis and presumably into synapsis with each other. But the reciprocal cross indicates, perhaps, that in the environment of the cytoplasm of this cross, they can not enter into synapsis. If this condition continues in later generations, we should represent the zygotes as AAA′A′, AAA′a′, AaA′a′, etc. This is the way in which duplicate genes have been represented previously as by Nilsson-Ehle, East and Shull. With this representation, heterozygotes of the form AAA′a′ could never give rise to recessives after selfing for any number of generations.

Which hypothesis is true in this case could easily be determined by experiment. The published results are not sufficiently explicit on this point. If the original cross were of the type AA × a′a′, producing in F_1 Aa′, the F_2, AAa′a′, would be a homozygote on the second hypothesis, and recessives should never

[1] *Proc. Roy. Soc.*, B 87, 1914.

appear. On Gregory's hypothesis recessives should appear in later generations. On the second hypothesis, homozygous races of the types AAa'a' and aaA'A' would be obtainable, in appearance like heterozygotes. These would breed true indefinitely when selfed, but should give recessives in F_2 after crossing, as in a case proved by Nilsson-Ehle.

SEWALL WRIGHT

BUSSEY INSTITUTION,
FOREST HILLS, MASS.,
June 19, 1914

NOTES AND LITERATURE

A STUDY OF DESERT VEGETATION[1]

Between three and four years ago Dr. W. A. Cannon, of the Desert Botanical Laboratory at Tucson, Arizona, visited southern Algeria in order to become acquainted with the more obvious features of the plant physiological conditions of the desert, and to make detailed studies of the root habits of certain desert plants. From Algiers the journey proceeded nearly due south about three hundred miles to Ghardaia, thence east about one hundred miles to Ouargla, and another hundred miles to Tougourt, returning through Biskra, and Batna to the northern coast. Throughout this long and wearisome journey the vegetation was studied in connection with the geographical and climatic environment and the results are brought together in a volume of somewhat more than eighty pages of text and thirty-seven plates, one of which is an outline map of the region visited.

Dr. Cannon speaks of the similarity of the flora of Algeria to that of southern Spain, France and Italy, where one is reminded of the vegetation of portions of California. Once in the desert on the way south low-growing shrubs on the plain become characteristic, including species of *Tamarix*, *Zizyphus* and *Artemisia*. Where water is available for irrigation, oases occur with their luxuriant vegetation of date palms, apricots, figs, mulberries, peaches, pears, oranges, as well as artichokes, beans, carrots, melons, peas, potatoes, squashes, etc. Further south the plain

[1] Botanical Features of the Algerian Sahara. By William Austin Cannon, Washington, D. C. Published by the Carnegie Institution of Washington, 1913.

is covered with small stones and pebbles and "not a tree, shrub, or herb appears to hide the bare ground. The mountains are naked rock, while the harsh outline of desert ranges and the distant low sand ridges give no evidence of plant life. But a closer examination of plain, dune and mountains reveals the presence either of living forms or of the dried remains of plants of a preceding moist season, in numbers and in kinds not at first suspected." All of which might well describe the desert conditions in our own southwest. This similarity is emphasized by the resemblance of many of the plants to those found in our Arizona deserts. Thus the "quidad" (*Acanthyllis tragacanthoides*) "has a very close resemblance to small specimens of 'ocotillo' (*Fouquieria splendens*) of the southwestern United States." And this resemblance extends to the structure of the spines and the return of the foliage after rains. It is interesting to note that the natives burn off its numerous spines, after which the stems "are eaten with avidity by camels," reminding us of the similar treatment and use of some cactuses in Arizona. Further to the south the vegetation is still more sparse and xerophytic, including *Ephedra, Retama, Haloxylon,* and among grasses, *Aristida pungens.* Near Ouargla, the southern point reached, there are places where no vegetation is present, as on the dunes, and yet on the fixed sand nearby were found *Euphorbia guyoniana, Retama retam* and *Genista saharæ.*

Much attention was given to the root habits of the plants encountered, and in the general summary which follows the account of the journey comparisons are made with the root habits of Arizona plants.

With this meager introduction we must refer the reader to the volume itself, which it is quite impossible to summarize in these pages. One thing impresses itself forcibly upon the reader, and that is that a desert is a *hungry place* in which the permanent vegetation maintains itself against plant-eating animals by a thorny or spiny protection. Yet Dr. Cannon points out that in this character of spininess the American desert plants excel those of the plants of the Sahara region.

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The University of Nebraska

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A COMPARISON OF THE RESPONSES OF SESSILE AND MOTILE PLANTS AND ANIMALS

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I. INTRODUCTION

During the past few years the attention of biologists has turned more and more from those phenomena which were supposed to be comparatively fixed, to responses to stimuli. Physiologists have long been concerned with the mechanism of response; psychologists are interested in its modification. Geographers, climatologists and ecologists have recently turned their attention to responses in natural environments and zoologists have become interested in response, particularly from the point of view of its specificity. In these quite independent investigations and compilations there has been little attempt at analysis with a view to determine legitimate lines of comparison among the exceedingly diversified types of organisms which have been investigated, and some confusion has resulted. For example, since the more obvious responses of plants are structural, persons not familiar with comparable phenomena among animals have made erroneous comparisons of sessile plants and motile animals. This paper is written to present in as nearly uniform terms as practicable (*a*) analysis of kinds or aspects of response, (*b*) justifiable kinds of comparison, and (*c*) the bearing of response phenomena on biological theory and controversy. It aims to show that the numerous kinds of response are reducible to a few simple types common to both plants and animals, and that the failure to consider all types has been responsible for confusion and various one sided theories. It further aims to show that study of response during the past few years has led to an unusual broadening of our conceptions.

II. BASIS OF DISCUSSION

As a basis for discussion we must first have a clear understanding of the character and definition of response. Secondly, we must determine what constitutes an individual in those plants and animals that are made up of repetitions of parts. Thirdly, we must note whether or not the organism is sessile or motile, capable of playing the part of either, or colonial pelagic.

1. Responses

The word response is used in various slightly different senses. In general it refers to more complex and time-requiring phenomena than "reaction." In geography the term has been used (Goode, '04) to cover all changes in culture supposed to be produced by climate or other geographic conditions. It is also applied by geographers and geologists to changes in the physical characteristics of man (evolution) which Goode ('04) has stated are slower than the cultural responses. In general botanists have used the term to cover changes of plant structure and function induced by external conditions. Cowles ('11), however, uses the word "reaction" to cover these phenomena. Coulter ('09) used the term response as synonymous with adaptation in plants. Zoologists have used the term to apply to changes in animals due to external conditions, but with little agreement as to what is to be included. We will use it *here* to include *reactions, changes in functions, structure, color, induced by external* conditions either directly or indirectly, without regard to how simple or how complex the processes involved may be.[1] The length of time required to bring the changes about may arbitrarily be taken as not exceeding the time required to breed five to ten generations of the species concerned. All organisms respond to stimuli because each stimulus acts upon some internal process. Strictly speaking, the response is the *change or changes in the physical or chemical processes of the organism* (*or the part or parts concerned*) *which results from the disturbance.*

Those things which we commonly see and term response are often the *later* and *less important* phases of the disturbance. The striking phases of responses of motile organisms are usually movements which follow closely upon stimulation. In sessile organisms the noticeable responses often appear only after a considerable period. In both sessile and motile organisms some responses are

[1] For good representative bibliography see Adams, '13, Ch. VIII and IX.

not evident because they concern internal, chemical and physical processes which affect neither form nor movement. Changes in the enzymes secreted by digestive glands, which accompany changes in food (Jennings, '06, p. 347), are examples. While thus recognizing that responses are concerned primarily with internal processes, we must of necessity refer chiefly to the external phases.

2. Sessile and Motile Organisms

Sessile organisms are those which are sedentary in habit, whether attached or possessing slight powers of locomotion. Motile organisms are those that habitually move about. Vagile or creeping forms as well as swimming, walking, flying, burrowing types are included. Most sessile animals are capable of moving their parts, while only a few sessile plants possess this capacity, and these only to a slight degree.

There is no sharp distinction between sessile (sedentary) and motile organisms. Every possible gradation exists between fixed non-motile types as *trees* on the one hand and the *pelagic fishes* on the other. It is the extremes which we will compare.

3. The Individual and Its Relations in Colonies and Groups

The following comparison of animals and plants is an attempt to distinguish potential or incomplete individuals in colonial organisms and compound organisms which, while not commonly recognized as colonial, are made up of incomplete individuals.

(*a*) *Animals and Plants made up of Single Individuals*

The vast majority of animals belong here. Most protozoa, solitary sponges, solitary hydroids, sea anemones, worms not preparing for asexual division, echinoderms, mollusks, arthropods and vertebrates. Only single-celled plants, young seedlings and possibly a few adults of multicellular plants which *possess* but *one growing point*

(exclusive of roots) belong in this group. *Single individuals* as described here are the basis for determining what shall be called individuals in *colonial* and *compound* types.

(*b*) *Colonial or Multiple Individualed Plants and Animals*

A number of animals and the vast majority of the plants belong here. The group can be roughly divided into two types, (*a*) those having a chain or plate arrangement of incomplete individuals and (*b*) those having a branching or tree-like arrangement. The groups of incomplete individuals of type *a* occur among the Protozoa, worms undergoing asexual reproduction, many of the Bryozoa and some of the Tunicates; both sessile and pelagic (plankton) forms occur. On the plant side type *a* includes plate-like colonies of algæ, filamentous algæ, some thallose plants and probably some of the fungi, though the great multiplicity of forms makes the separation of this group from the branching tree-like types, difficult.

Type *b* includes some of the colonial Protozoa, the majority of the sponges, hydroids, corals and the branching Bryozoa. The algæ, fungi, mosses, ferns and flowering plants are all represented. The colonies are usually attached to the substratum (sessile).

i. *Numbers of Individuals.*—Among the animals the number of so-called *zooids* is the number of incomplete *individuals*. In the sponges there are as many zooids as there are *excurrent openings* (osculæ) (Minchins, '00, p. 91). Zooids usually possess a mouth opening and organs for securing food, though in some cases they may be specialized for reproduction, defence or locomotion as in some of the Cœlenterates. Among the colonial plants there are as many incomplete individuals as there are *buds* or *growing points* (vegetative regions). There are no regularly occurring organs in animals, strictly comparable to leaves. However, any organs such as tentacles, gills, etc., which secure or absorb nutriment may be re-

garded as *analogous* to leaves. *Each potential bud with its leaf may be compared to a zooid.* In comparing plants and animals, *roots can perhaps be compared with the holdfast organs of hydroids.* In both groups, roots and root-like organs are individuals of a very *low order of individualization* and of a type not well represented among animals. The holdfast organs of animals are not important absorbers of food and water.

ii. *Stems and Other Connecting Organs* (*Conducting Tissues*).—The most striking difference between the incomplete individualed or colonial plants and colonial animals is the presence in the former of specialized stems and highly complex conducting tissues (Cowles, '11; Pütter, '11, pp. 361–66). The conduction of food materials from the root to other parts of the plant and from the leaves to the root is a functional necessity not paralleled even in those colonial animals showing the greatest division of labor. In animals stems are relatively undifferentiated and are often made up of living, relatively unspecialized zooids, as, for example, in many *Bryozoa* such as *Crisis.* The tendency to cauliflory in some plants and the ability of cambium to produce shoots and of the stems of most hydroids to produce individuals indicates that such a condition may be potentially present in all. In stalked *Protozoa* the stems are solid, while in most Cœlenterates they are tubes, usually simple though sometimes complex, made up by mere elongation and branching of the stock of the simple single forms such as the *Hydra.* The lumen is usually ciliated and makes possible a transfer of material which renders practicable such division of labor as occurs in this group (Pütter, '11). In the *Bryozoa* the different zooids have their body cavities joined in the simpler forms merely as a branching lumen of the main wall of the colony; in others by small openings the more specialized of which are sieve-like plates (Harmer, '01, pp. 471 and 496; Delage and Herouard, '97, Vol. 5, p. 62).

The connection between the individuals of the tunicate colonies is often very complex, due to the fact that in the

most complex types the stolon (stem) gives rise to new individuals and possesses all the layers of cells which take part in forming them. The connection between different individuals differs in different groups and is determined by the particular mode of asexual reproduction. As the individuals are quite independent of one another in function, these connections do not have the same significance as in plants. Even where there is a common blood circulation, as for example in the *Clavellinidæ* (Harmer, '04, p. 71), there is no noteworthy division of labor.

iii. *Metabolic and Reproductive Relations of Individuals.*—The flat worms at certain times consist of chains of zooids at various stages of development and with various degrees of independence. Child ('13) has found that these chains of zooids present a series of gradients in rate of metabolic reaction. The rate is highest at the anterior end of the whole chain and decreases toward the posterior end, not uniformly, however, for the rate is *lower* immediately in front of each head region than it is in the head region itself. A gradient is present in the axis of each zooid. The most anterior head dominates so long as the chain remains intact. In the corals certain zooids dominate (Wood-Jones, '11) over the others. Some types have a single dominant zooid and some more, while in other cases all are equal.

Among plants whose form is that of a chain or a plate the individuals are less closely bound together and dominant vegetative regions are probably less well developed. In the branching types, dominant vegetative regions occur (Cowles, ''11, p. 747; Goebel, '00, Vol. I, p. 206). In the conifers, for example, there is a leader, a dominant growing region at the tip of the main stem just as in certain madrepore corals (Wood-Jones, p. 83). Other plants like the elm have *several* vegetative regions which dominate over others, as they do in the branching madrepores.

Growth form or colony form varies according to certain laws dependent, in part at least, upon the metabolic

relations of individuals. Thus Wood-Jones says of the corals—

a colony may grow according to five different types of vegetative growth . . . it may grow as (1) a spherical mass, (2) an encrusting layer, (3) a free plate, (4) a branching tree-like growth, or (5) a mere amorphous lump.

He further notes the division of all the corals into two groups of normal growth-forms; for *all the zooids may take an equal share* in the asexual reproduction or, again, *some may be of greater importance than others*, and the asexual reproductive functions may be lodged in a very few individuals only. Considering the first division (all zooids taking equal share, the principal types of budding vary from each other in the actual site of origin of the daughter zooid from the parent, in the degree of final separation of the two zooids, and in the thickess of the intervening partition between the two zooids. The amount of rising above the general surface by each individual zooid is likewise subject to variation.

Turning now to the corals that constitute the second class (some zooids of greater importance than others) which in the words of Wood-Jones have some of their units specialized as active agents of growth,

it is at once seen that the possibilities of variation of normal vegetative habit are greatly increased. All the elaborate branching forms, plates and leaf-like growths belong to this class; and all are evolved by special peculiarities of the growing point. The zooids that constitute the growing point may take various forms; they may be arranged as a cluster, as a creeping edge, or as many varieties of terminal shoots of branches.

In the first instance, it is necessary to draw very sharp distinctions between two subdivisions of this group. In *Group 1* come all those forms like *Montipora,* whose distal zooids are the newest formed members of the colony; and in *Group 2* are included the *Madrepora,* whose distal zooid is the most ancient individual in the whole group.

In dealing with *Group 1* many forms have to be considered, for when the youngest are the active zooids their growth cluster may be variously disposed, and on its disposition the resulting vegetative form entirely depends.

In *Group 2,* however, this state of things is entirely altered, for there one zooid, which is situated at the extremity of the stem, and which I

shall call throughout the "*dominant apical zooid,*" constitutes the growing point; and this zooid is the parent of the entire colony.

Various writers make comparable statements or show comparable principles among hydroids (Motz-Kossowska, '08) and Bryozoa (Davenport, '91, et al.) and among plants (Goebel, '00). Of the colony form of the tunicates Herdman ('04, p. 82) says:

> The marked differences in the appearance of the colonies of compound Ascidians is largely due to the methods of budding; even in those of stolon type where the budding is practically the same in essential nature, the results may be different in superficial appearance, according as the buds are formed on a short stolon close to the parent body, or from the extremity of the post abdomen or from the long epicardiac tube which may extend for some inches from the ascidiozooid.

Thus we conclude that the innate causes of different growth-forms (colony forms) of colonial organisms are (*a*) the *mode of division of the zooids* or vegetative regions, (*b*) the *ratio of stem elongation to number of zooids* or buds produced or uniformity or lack of *uniformity of stem elongation* (Wood-Jones, p. 76) closely related to (*c*) the presence or absence, *number, position* and *region* of influence of the *dominant growing* regions or dominant zooids, and (*d*), in some cases, the *grand period of growth* and the *length period of the internodes* (Johnson, '11). The innate tendencies are thus reducible to a few principles applicable to both plants and animals.

(*c*) *Responses of Motile Organisms*

i. *Movements.*—In motile organisms the most striking responses are changes in position brought about by movements usually more or less random, and which bring the organism into various conditions one of which usually relieves the disturbance. The organism resumes normal activity in conditions which brought the relief (Jennings, '06). These conditions are not necessarily advantageous, but are usually so when the stimuli are those encountered in nature (Mast, '11). Behavior of motile organisms is also modified by repetition of action even in animals as low in the animal series as the *Protozoa* (Holmes, '11).

Jennings ('06) has quoted various botanical workers' observations on motile plants the behavior of which probably follows the general laws governing the behavior of motile animals. As a result of the quick behavior responses of motile organisms, their distribution at any given time is a better index of the conditions at that time than the distribution of sessile organisms, because when the conditions at a given point become unfavorable the motile organisms usually move to another situation, while the sessile forms remain and perhaps die.

ii. *Structural Responses*.—Among motile animals, structural and color changes occurring as a response to environmental conditions (stimuli) are usually not of importance to the organism concerned. The color differences induced in *Lepidoptera* by heat and cold (Stanfuss; Fischer) and the structural differences in Crustacea such as were brought about in *Cladocera* by Woltereck, and other modifications brought forward recently, are usually of no known advantage or disadvantage to the animals concerned (Bateson, '13, Ch. IX and X). Such responses in color and general form do not ordinarily take place in adults subjected to such conditions. The striking structural responses of motile animals are often responses to the organism's activity. The use and disuse phenomena of the Lamarckians, the increase in size and form of muscles, thickening of skin in man and mammals, are well-known examples of a type of responses which have influenced zoological speculation. Child ('04) controlled the form of *Leptoplana* by controlling activity. Holmes ('07) found that the movements of pieces of *Loxophyllum* have an important part in shaping the general outline of the bodies of the resulting forms. The general forms of motile animals are correlated with their activities but whether form or structure correlated with it appeared first in the course of evolution has been the subject of considerable fruitless speculation.

(*d*) *Responses of Sessile Organisms*

i. *Structural Responses.*—The striking phases of responses among colonial sessile organisms are often changes in form and structure, or the relative position of the parts. The changes in structure or position of parts are not necessarily advantageous or useful, but are usually so when the stimuli are those commonly encountered in nature (Cowles, '11; Loeb, '06, p. 124; Wood-Jones, '11; Ch. VIII). Indifferent and detrimental responses are often given under experimental conditions and no doubt the absence of such variants among sessile animals collected in a wild state is due in part to the failure of such organisms to survive. A few sessile colonial organisms such as cacti (Cowles, '11) show little or no plasticity.

Among sessile animals, the observations of Wood-Jones form the best examples of response. He found that the branching type of corals dominated in barrier pools, tall slender non-branching types in deep water, and massive boulder types on surf beaten shores. Thus he figures similar colonies of *each of three genera* which, while possessing certain peculiarities of their own, are in general agreement as to *growth form* just as sessile plants usually are; and this in part for comparable reasons. Thus various conifers occur as *Krummholz* in the high mountains, due to severe conditions (Cowles, '11, p. 732), wind, snow, and in part to the injury of *terminal growth regions* of the main stem which gives rise to lateral branches. The boulder-like corals with the zooid at the same level occurring on the surf-beaten shores of coral islands are due, in the case of Madrepora, for example, to repeated injury of the *terminal dominant zooids.* Conifers in protected situations often grow into *tall slender trees* comparable with the (deep) *still-water corals.* The barrier pools afford conditions where the terminal buds are less often injured than in the surf and the tree-like branching corals result from minor injuries to dominant zooids.

Wood-Jones finds further that still-water corals are less strongly calcified than those in rough water, the strains producing increased secretion analogous to increased tissue production as a result of mechanical strains in plants (Cowles, p. 669). Corals show different kinds of growth under different environments particularly when injured. The new part may be different from the rest and adjusted to the environment thus making it appear as though two "species" occurred in the same colony. The mode of division of the zooid is also different under different conditions. Plants show similar variation with changes of conditions, particularly in the leaves which are *divided* in submerged portions of amphibious plants and entire in the emerging portions (Cowles, '11, p. 595).

As has been noted, there is nothing in sessile animals that is more than roughly analogous to leaves. Leaves show marked structural differences on different parts of the same tree where the environmental conditions are different, as, for example, in the differences which occur between the upper and lower portions of a forest tree. While there are, no doubt, differences in similar details (histology) in the organs of display in different parts of the same colony of sessile animals, little or nothing has been done upon them. As a further indication of the prevalence of structural response in sessile organisms of the hydroids Hickson states that there is probably but one species of *Millepora* which occurs in a large number of growth forms. The commercial sponges (Moore, '08) and common freshwater sponges and polyzoa show many different forms under different environmental conditions.

The major differences in growth form induced by external stimuli in colonial organisms result from modifications of the rate and character of growth with respect to the *four innate* tendencies toward various growth or colony forms discussed above, and which may be briefly enumerated as follows: (*a*) mode of division, (*b*) amount of stem elongation, (*c*) influence of dominant regions and

(*d*) grand period of growth and the length of period of internodes.

The principles are concerned with asexual reproduction and apply to motile organisms only exceptionally as for example in the case of colonial pelagic forms. The laws are applicable to both plants and animals.

ii. *Movements.*—Movements of sessile animals are usually contractions or extensions of parts or of the entire body. Tentacles and comparable organs are capable of movements for securing prey. Such organs often tend to wrap about objects which are in motion. Many sessile animals are capable of opening and closing a mouth opening and of bending or twisting the entire body. Plants possess a comparable capacity only occasionally.

(*e*) *Behavior of Sessile Motile Organisms*

Most sessile animals are capable of some movement and react by contraction of parts. The reactions may be modified by repeated stimulation (Jennings, '06) and usually by physical factors. Some animals, as *Hydra, Stentor* and many others are both sessile and vagile or free-swimming, and show different types of behavior when attached and when free. Jennings states that such protozoa have a more complex behavior than motile forms. This is due to their combining the types of behavior of sessile and motile animals.

(*f*) *Response and Taxonomy of Sessile Organisms*

Hickson ('98) has stated that there is but one species of *Millepore* and believes that sex organs will be found to be the best taxonomic characters. Wood-Jones states that there are far fewer species of corals than has formerly been supposed, and states further that growth form can not be used to distinguish species. Among fresh-water sponges and Bryozoa reproductive bodies (*gemmules* and *statoblasts*) have been found to possess satisfactory taxonomic characters. This is a situation quite parallel with that in plants where reproductive

organs are used as classification characters. The ideas of the reproductive organs of plants are now at the "fixity" stage which on the animal side is paralleled by the idea of fixed tropisms and fixed instincts, of a few years since. Variability of tropisms is now well recognized and reproductive organs in plants are being found plastic, as those of animals will probably be found also.

III. Parallelism between Sessile and Motile Organisms with Reference to Ecology

From a summary of the considerations above it will be seen that for practical comparison the *division of organisms into plants and animals may be abandoned and only reference to sessile and motile organisms made.* We may now turn to a discussion of a few general principles making the division into sessile and motile organisms only. The behavior of motile organisms is plastic. There are innumerable cases of modification of reaction by variations of physical factors (Jennings, '06; Loeb, '06; Mast, '11). If for purposes of discussion we put the usual "normal" reactions of motile animals over against "normal" structure of sessile animals, we note that the *behavior response* of the former *parallels* the *structural response* of the latter.

1. Breeding

Motile Organism	*Fixed (Sessile) Organisms*
(a) The breeding activities take place within narrower limits than any other activities. Merriam, '90; Herrick, '02; Reighard, '08; Shelford, '11*a, b, c,* '12*a, b.*	(*a*) Breeding and other activities within same limits, except that dispersal may take place over wide areas through detachability of seeds and other reproductive bodies.
(*b*) The selection of breeding place and breeding activities, including first activities of the young, are governed by the same general laws as other activities.	(*b*) Less marked because a selection of abode by sessile organisms takes place through the behavior of motile young stages or through wide dissemination of non-motile bodies by wind (etc.) with growth under favorable conditions and failure elsewhere.

(*c*) The breeding activities are probably least modifiable and least regulatory.

(*c*) The reproductive organs and early embryonic stages are less modifiable than the vegetative parts.

(*a, b, c*) The maple tree, a sessile organism, is entirely stationary in its adult stages. The seeds are blown by the wind. One would not accomplish much in the study of ecology by studying the distribution of the seeds of the maple, or, on the other hand, by the study of the distribution of adult birds, without some further discrimination.

Sessile organisms are not difficult to associate with their proper environmental conditions in their adult stages. As we proceed in our study to forms which can move readily and rapidly, the difficulty of associating them with their definite environmental conditions increases. Sessile organisms have stages which are small and capable of easy dispersal, as in the case of the maple. Sessile marine animals and some sessile plants frequently have motile forms in young stages. In these motile stages they are governed by the same laws as other motile organisms. The conditions under which the motile stages develop into the sessile forms are crucial.

Most fresh-water forms and some marine forms of sessile organisms are without the free-swimming stage, and they produce non-motile stages physiologically comparable to the seeds of higher plants. The winter bodies (statoblasts) of the Bryozoan (*Pectinatella*) common near Chicago, and which is a strictly sessile organism, are comparable to seeds and probably require "ripening" by cold, just as do many seeds and the reproductive bodies of some other species of the same group. Organisms which are highly motile in the adult stages are not motile in the egg and young stages. The eggs and young of birds, for example, do not move about, yet birds are the most motile of all animals.

2. Comparison of the Sessile and Motile Elements of the Biota

(*a*) The motile organisms of a given habitat usually react simi-

(*a*) The sessile organisms of a given habitat (particularly plants)

larly to two or more stimuli not differing greatly in intensity from their optimum, *i. e.*, the percentage of positive or negative trials is essentially the same for standard intensities. There is also probably similarity in the rates of metabolism, etc.	usually show similar functional rates, such as similar rates of transpiration among sand dune plants.
(*b*) The *specificities* of *behavior* such as the mode of *moving* the organs, *e. g.*, of locomotion, and in some cases the combined results of *different behavior reactions* are similar and hence are *ecologically* equivalent. The size and efficiency of the organs are also involved.	(*b*) The various structural devices which meet the conditions of the environment are ecologically equivalent.

A testing, for example, of the rheotaxis of a large number of brook-rapids animals has shown them to be strongly positive, and when active individuals only are considered the percentage of positive trials is very similar for the entire rapids community. Likewise they are in accord in their avoidance of sand bottom. Many of the animals have special means of attachment which may be brought into play with speed.

As has already been pointed out elsewhere, ecological equivalence is illustrated here. The darters (fish) are strong swimmers and are able to live in rapids by virtue of their swimming powers and positive reaction, while snails meet the same general conditions through positive rheotaxis and the strong foot which enables them to hold to rocks.

3. Sessile and Motile Organisms in Ecological Succession

(*a*) Ecological succession is succession of ecological (physiological) types over a given area, due to changes of conditions which both cause migration of physiological types and transformation of such types as remain (Shelford, '11*a*, '11*b*, '11*d*, '12*a*, '12*b* and citations). Changes of conditions are geographic, *i. e.*, physiographic, climatic,

etc., and biological (due to organisms). Sessile plants are the chief biological cause of succession on land and in fresh water, while sessile animals are the chief biological cause in the shallow portions of the sea, especially in coral reef regions (Wood-Jones, '11). Sessile organisms are more important causes of succession than motile ones because they (*a*) build up the substratum with detritus and skeletons, (*b*) interfere with the movement of the surrounding medium, (*c*) cut off light from the substratum where other organisms must reside and their own young secure foothold, and (*d*) they usually affect their own environments with excretory products more than do motile organisms. In general we recognize ecological succession of motile animals through the differences of behavior which accompany changes in conditions. The differences are physiological; differences in behavior are the easiest index of the physiological condition. The character of nests, burrows, etc., are often good indicators also.

IV. INFLUENCE OF RESPONSE PHENOMENA UPON BIOLOGICAL THEORY AND CONTROVERSY

A glance at some aspects of biological speculation since before the publication of Darwin's "Origin of Species" is essential to our understanding of the attitude of biologists until recently, toward responses.

1. Teleological View

In the matter of animal behavior response, the earlier workers interpreted the reactions as intelligent and purposeful, ascribing human sensations, etc., to animals as low in the scale as protozoa. This teleological tendency was paralleled on the plant side by the idea of purposeful adaptive responses. Many common plants respond (structurally) readily to environmental conditions. As has been noted, the commonest of the surviving responses of the wild state are apparently advantageous. This led some botanists to a Lamarckian teleological conception of response, perhaps best represented by Kerner and

Oliver's work on the natural history of plants. According to this view, responses are advantageous and for the *purpose* of *preserving* the plant. Thus response and adaptation become synonymous (Coulter, '08), a usage quite inapplicable to animal structure. At the beginning of the recognition of the response phenomena of corals Wood-Jones takes essentially the view of adaptation which botanists have tried and rejected.

Lamarck, who was for many years engaged in botanical work, must have noted many cases of advantageous structural response in plants. Later he undertook the study of invertebrates which show great plasticity, and was naturally much influenced in the development of his theory of transmutation of species by the response phenomena in the plastic organisms which he studied. Thus the responses of motile (as well as sessile) organisms which result from their own activities or the action of their environments formed an important feature of Lamarck's (Packard, '01; Cope, '96) theory of transmutation of animal species. His theory is clearly in accord with the material he studied most. The nature of his contention and various well-known circumstances caused his ideas not to be accepted.

2. Natural Selection View

Characters used in classification of motile animals before and since the time of Darwin are quite frequently adaptation characters. Thus the large pectoral fins and absence of an air bladder are characteristics of an entire group of fishes, the darters. The divided eyes of the *Gyrinidæ,* which swim at the surface of the water, are so adjusted that one half looks downward into the water, and the other outward into the air. This character combined with the paddle-like hind legs would have served to distinguish the family. Again larvæ with a head and thorax modified to fit a circular burrow and with hooks on the dorsal surface of the fifth abdominal segment, which is supposed to be an adaptation to prevent the animals

from being drawn from their cylindrical burrows by their prey, could serve to distinguish the entire family of *Cicindelidæ* (tiger beetles). Such cases might be multiplied indefinitely.

Following Lamarck came Darwin, who, being more particularly a zoologist, was probably (proportionately, at least) less familiar with structural response phenomena. He was apparently impressed with the "fixity" of the so-called adaptation characters in motile animals, and with the fact that they are often family, generic or specific characters. With the assumption that they originated in the environment in which they are now found, Darwin and his followers on the zoological side credited "natural selection" of structural characters with the origin of species. Though broader than Lamarck, this important feature of Darwin's theory was quite clearly drawn from data on motile animals. After the acceptance of Darwin's theory, biologists were for many years engaged in elaborating the ideas of phylogeny and natural selection by working out recapitulations and homologies and by pointing out cases of adaptation. The investigation was largely confined to the highly individuated animals. The morphological method of this period, which indeed has still continued in use among a minority of zoologists and which finds a parallel in the recent morphological study of the sex organs of plants, belongs to descriptive rather than to analytical science. Since its conclusions are often based upon the arrangement of species or of stages in development into series chosen by the investigator, it is a method which often allows free play of subjective fancy. Thus unconsciously experimental study of modification by environment became more and more neglected, and the dominant type of investigation being such as to show only the usual course of events in development, the ideas of fixity grew more and more. Thus the fact that the external form, structure and color of animals are not easily modified without careful experimental methods, and that the structural responses of sessile animals were

so little known, resulted in structure in animals being frequently regarded as fixed and every resemblance and peculiarity being too often regarded as significant. The explanations of supposed adaptations among animals fell largely to the theory of natural selection which was strained by some (see, for example, in Romanes, '92, p. 269) to explain origins in great detail, largely on the basis of the competition of species for food, etc. Explanations along this line were *carried to a reductio ad absurdum* as indicated by Livingston ('13) and have by no means disappeared from the scientific calendar. This tendency was less important on the plant side. More attention was given to speculation concerning adaptive response.

From a consideration of the facts just presented, we note that the characters of the two leading early view points in evolution were no doubt influenced if not actually caused to crystallize into their peculiar form by the failure of workers to recognize the entire series of phenomena which we have presented above. Thus a review of the responses of sessile and motile organisms throws much light on the influences leading to the first conceptions and later modification of these two leading doctrines. Botanists for many years dwelt mainly on the response of sessile organisms and crystallized a Lamarckian conception of the origin of adaptations through the fixing of advantageous responses as hereditary characters. During the same period zoologists essentially ignored sessile and other multiple individualed animals and their great plasticity and crystallized the Darwinian idea into Weismannian germplasm doctrine based on highly specialized single individualed animals.

3. Supposed Non-Inheritance of Response and the Germ Plasm Doctrine

The theory of the independence of the germ-plasm from the soma, and its continuity from generation to generation, was brought strongly to the attention of zoologists in 1885 by Weismann. It was the natural outgrowth of the methods and theories of the preceding period and

was largely based upon the non-inheritance of mutilations and the fact that the germ cells of a few organisms are, morphologically, early differentiated from the soma. Turning to its influence upon ideas concerning response, we note that from this viewpoint details of structure were not of fundamental importance unless traceable to the germ plasm. Still, structural details were more important than response, because, with the exception of instincts, responses were believed to occur *independently of the germ plasm* and hence were of interest only on their own account. Thus the methods used in applying Darwin's theory led to neglect of experimental study of response and culminated in the extreme views of Weismann. The germ-plasm theory or the ideas of heredity which are associated with it has dominated zoological thought almost if not quite down to the present day.[2]

4. The Influence of the Study of Response on Present-Day Biological Theory

One of the most striking developments of recent years has been the discovery that behavior responses are modifiable to a high degree. Small traces of reagents reverse

[2] Unconsciously suggestions of the supernatural which come up in connection with heredity and evolution have stimulated investigators to study and speculation, though they have often approached the question of heredity with an unscientific attitude. This is indicated by such statements as "I could not, however, resist the temptation to endeavor to penetrate the mystery of this most marvelous and complex chapter of life" and "the momentous issues involved" and "no more fundamental problem could well be stated" bear out this statement. The ardency which appears here and elsewhere in the discussion of scientific questions, appears to the writer to be associated with the discussion of problems which can not be referred to existing facts for solution. Few of the present generation of scientific men acquired a working knowledge of the methods of science before the age of twenty-five years, and the early habits of mind were formed in the atmosphere of the supernatural and dogmatic, which has characterized human thought for centuries. It is doubtful if the majority of us can maintain a scientific attitude for more than a short period; we must constantly come back to our tests and principles. This may account for many of the contradictions regarding scientific principles which one finds in the conversation of scientific men. When the methods of science have become the methods of society we may expect a group of scientific men far more effective than we ourselves can hope to be.

reactions. Intelligent behavior occurs in the lower Arthropods. Even *Paramœcium* shortens the time required to turn around in a tube, by repetition. Actions formerly regarded as instinctive now appear to be mere innate tendencies perfected by repetition. Thus the ideas of fixity have essentially disappeared from this field.

The response of organisms to injuries and the general control of form in the lower groups has done much to break down the ideas of fixity developed by Weismann and embryological schools. Thus Child, the leading American worker in this line, is able to control size, form, number of eyes in the case of Planarians. Various writers have found modifications inherited after several generations of repeated stimulation (see Bateson, '13). The development of anti-bodies (immunity) has been shown to be a response occurring in connection with many normal processes. The discovery of responses of so many types has led to abandoning ideas of fixity even among students of embryology and genetics. Thus we note the recent decline of the doctrine of continuity and independence of the germ plasm and kindred doctrines and points of view, which constitute the central ideas of fixity. It will accordingly be profitable to consider some further facts which make the germ-plasm doctrine unnecessary.

5. Aspects of the Untenability of the Germ Plasm Doctrine

The presence of primordial germ plasm is assumed even in sessile colonial organisms such as plants, cœlenterates, and in flatworms, etc., where under certain conditions any small part of the body may give rise to a complete organism. Here the theory is not needed to explain the facts.

Child ('11) said:

> The theory of the continuity of the germ plasm as a system, independent of the soma, except as regards nutrition, has played an important part in biological thought during the last two decades, but I am convinced that it has led in the wrong direction and that it is re-

sponsible for many pseudo-problems of heredity and development, which on the basis of a different theory could never have occupied the attention and wasted the energy of biologists. Briefly my position is, that the gonad primordium is, at least up to a certain stage of development, physiologically a part of the individuality as are other organs, and that its further history of differentiation into male and female gametes indicates that it becomes specified in a particular direction, at least partly in consequence of its correlative environment in the organism.

The independence of the germ plasm is not well supported physiologically. Thus Wilson ('12, p. 163) says of the effect of prolonged ingestion of alkaline salts by mice:

> No obvious changes were evident in the liver, kidneys, lungs, spleen and intestines but in the testes some extraordinary alterations were found. These results are of especial interest because as the cells of the testes except the basal cells are regarded by many cytologists as out of coordination with the somatic cells. As a result of these experiments it would seem that they are more susceptible to changes in reactivity than the surrounding plasma.

Dungay ('13) and authors cited have thrown comparable light on this question.

The facts of embryology themselves are but a pseudo argument in its favor. The organisms in which continuity is supposedly demonstrable are highly individuated and their organs highly specialized and many different organs are early separated from the common mass of cells. The germ cells thus follow the general law of development in such animals. The germ plasm is probably no more independent of other parts of the organism than is the liver or any other special tissue. "Germ plasm" and "germinal continuity," if such exist, may thus be merely incidental to the particular type of organization of the specialized individuals in which they occur.

It should further be noted that on the botanical side this doctrine of the independence and continuity of the germ plasm has received little attention and has been given little credence because "germ plasm" arises from different tissues and is neither set aside early from the soma nor is it in any other sense clearly continuous.

Furthermore, the plasticity of plant structures made the application of the doctrine of natural selection to supposed adaptations untenable, and this type of explanation has received little more attention with botanists than have Lamarckian speculations with zoologists. The adaptation characters of plants can not ordinarily be used as taxonomic criteria (Coulter, '08).

6. The Measure of Values in Biological Science

One hears reference to pure science as something quite apart from applied science. It is indeed true that investigators in pure science are to some degree prompted to push forward in research by interest in the problems for their own sakes. But the human mind does not work long isolated from practical affairs or the main channels of human interest, and it is doubtful if the pure-science investigator continues long in this way. Observations are soon connected up in some way, actual or possible, with some human interest, be it as remote as the improving of human stock in remotely future generations. Thus "*pure science*" defined as investigation for investigation's sake hardly exists so far as the pure-science workers are concerned, but may be best defined as an *indirect* method of attacking problems of general importance. It differs from applied science in that application to practical problems is not its aim, though the estimated value of theories and results in "pure" science are often greatly modified by applicability to practical questions.

Certain problems and groups of facts in biology are sometimes referred to as *fundamental*. Some one has said that a fundamental problem is one the solution of which biologists have decided will give greatest progress. It is doubtless true that a few leaders reach such decisions with regard to particular questions, but the real causes of their general acceptance as fundamental are social and imitative. Thus when one investigator or a small group of investigators arrives at such a decision many others usually become active along the same lines largely because it is a popular topic. Thus under the influence

of a group of investigators among whom Weismann was a conspicuous leader, problems of the germ cells, the egg's early development, and heredity, became "fundamental problems." They evidently argued that since all comes from the egg and germ cell, all must be discoverable in the egg. If germ plasm were as independent from soma, as completely insulated from environment as continuous from generation to generation as has been assumed, the study of germ plasm would be the only way to the solution of the problems of heredity and evolution. This follows no matter whether the chromosomes or almost the entire egg are credited with carrying hereditary qualities; only the postulation of continuity and independence from soma and insulation from environment are necessary. If the independence of germ plasm from soma be accepted even in a weakened and modified form it follows that studies of somatic characters can at most be of secondary importance from the point of view of heredity and evolution. Thus in some quarters the value of various lines of zoological work has been estimated largely, unconsciously, no doubt, in proportion to the nearness or remoteness of their relation to the "*germ plasm*" question.

Thus it is true that in biology as in all other fields values are measured consciously or unconsciously by criteria. In recent years another better criterion of value has made its appearance among zoologists. The germ plasm criterion already discussed was primarily morphological; the second is physiological, borrowed no doubt from physiologists. It measures values on the basis of the analysis of the organisms into terms of physics and chemistry or is concerned with a mechanistic conception of life in all its manifestations. From this viewpoint the study of each and every part of the organism is important because the discovery of laws governing one part is usually or at least often of general importance. Investigations from this viewpoint have shown that the germ plasm criterion is clearly illogical in its application to the study of somatic characters because it is based upon the

tacit assumption that the soma is governed by *different laws* from the living matter which makes up the germ plasm from which it arose. In other words it is assumed that the germ plasm is so *different* from the soma that the discovery of laws governing the soma is a type of investigation of relatively little significance.

Some criterion of values is of course necessary in science as well as elsewhere, and for the sake of argument we would be willing to accept the second when broadly stated and the first when broadened and modified so as to accord with the second as appears to be the case among certain students of genetics. In other words, problems of the germ cells, the egg, and heredity, are of much importance when the germ cells themselves are regarded as dynamic and in their relations to the dynamics of the organism as a whole.

Granting that these are true and tenable criteria of values in present-day biological science, what is to be the method of application? Should biology demand that results be of direct application to these "central" problems? One has but to look at the history of almost any branch of science to find that great, if not the greatest, advances have come through following up results at points where relations to the central problems of the period were quite unsuspected, or by the transference of methods, principles and results from one field to another where relations between the two were not suspected. Take, for example, immunity and immunization, the history of which is ably sketched by Adami ('08, pp. 451–528). It has been known for ages that one attack of many infectious diseases yields more or less complete immunity from subsequent attacks. Thus for centuries in India and the East individuals, chiefly children, have been purposely inoculated with matter or by contact. The practise grew out of experience showing that diseases thus communicated to healthy individuals from weaker ones are less severe. In 1796 the results of Jenner on vaccination with cowpox were published. This may have influ-

enced Pasteur, who over eighty years later laid the foundation for the modern epoch of development, by combating a plague of diarrhœa in poultry (1880). During the twenty years following, various investigators added noteworthy contributions, and about 1900 Ehrlich and Morgenroth evolved the "side-chain theory" by which a large number of possible conditions can be predicted and all the observed facts of immunity explained. While not expressed in strictly chemical terms, the theory and the experiments which support it are very important both practically and theoretically. In recent years the knowledge of immunity and comparable phenomena have been greatly extended. Various workers (Pfeffer, Vol. II, p. 262) have shown similar phenomena in the increased resistance of plants to poisons, thus making the responses of plants and animals still more generally comparable. Most recently workers on problems such as fertilization (Lillie, '13), standing in close relation to the older germ-plasm doctrine, have discovered facts belonging to this field and made use of Ehrlich's theory to explain the observations. This development has helped to confirm the conclusion of some investigators that immunity phenomena represent important features of the chemical mechanism of life. Adami has remarked,

> That a plague of diarrhœa in a poultry yard, studied by a professor of chemistry, should be the seed from which has grown the vast development of later years is a strange fact, but a fact nevertheless.

What was the attitude of pure science so called, of germ-plasm doctrinairies, and biologists generally during the long period which elapsed before they could make use of his results? Clearly it was one of indifference, if not disgust, toward the subject. The probable result of such attitudes on the progress of the investigation of immunity phenomena, had it not been for their immense practical significance, is clear. They could not have received their proper share of attention. Thus in the pursuit of the analysis of the chemical mechanism of life men who sought it directly have failed in this one impor-

tant step, and the chief contribution has come from very remote indirect methods. Generally speaking the investigators who choose a direct method of attack often put themselves somewhat in the position of the chemist who would make chemical analysis of *living* matter when his *first* step *defeats* its own purpose by killing the substance to be analyzed. The failure of exclusively direct methods is often evident. Still the ability to obtain results by the method of direct attack, combined with a far too rare ability to tie with them indirectly obtained data, sometimes gives noteworthy contributions.

It accordingly remains to be seriously considered whether or not biology can afford to apply criteria to the measure of the values of investigation. Their application is of course largely unconscious, but the effects are not thereby modified. Noteworthy results of their application are (*a*) concentration of work in certain lines indicated by a given criterion, and (*b*) an actual abandoning to a large degree of remote and indirect methods of attacking the problems which the criterion involves. This means the partial abandoning of the methods for which pure science stands.

Criteria can be safely used only in a very broad general way, and in application more often to past progress than to current investigation. They are perhaps most valuable as a guide to individual investigators working on problems remote from these more or less central "pure science" questions. That some guide should be in the hands of such workers is beyond question. In the hands of those attacking the problems directly they often appear detrimental because they soon take on an extreme form and become regarded as fundamental. At this stage they are usually in need of extensive revision. If the investigator is contributing observations and details only, he is doing a great service, for such information is needed everywhere. If he is able to combine his own and others results, he almost invariably draws data from all sources, *direct* and *indirect,* far and near. Granted the

ability to synthesize, the opportunity to use the ability sometimes comes to those who attack the so-called central problems directly. It comes equally often (we believe more often) to those who have led up to the central problem from some remote viewpoint, frequently condemned by the followers of direct method of attack. Granting the importance of synthesis, if the biologist seeks the solution of such a problem as the germ-plasm problem, he should encourage workers to start at points as *remote* from the subject as possible, that they may *approach it with new light and from new angles.*

In judging the work of another, its value should be determined more by the (*a*) strictness of scientific method used, (*b*) the thoroughness and completeness of the investigation, and (*c*) (and perhaps most important of all) evidence of ability to synthesize and combine other results with his own with a view to broader generalization. It must, however, also be recognized that there are many biological problems of much human importance, which must be solved quite independently of the ideal central problems of pure science.

6. Summary and Conclusions

From the data presented above, we note that the doctrine of purposeful, advantageous response (including anthropomorphic ideas) arose from the uncritical non-experimental study of the responses (structural) of sessile and (behavior) motile animals. The idea of the all-sufficiency of natural selection is largely the outcome of observational study of apparently fixed and yet apparently adaptive characters of *motile* highly individuated animals. The doctrine of the continuity of the germ plasm is likewise the outgrowth of the study of highly individuated animals in which the various organs are early differentiated in the dividing egg. No one of the doctrines is wholly tenable; no one is more than a partial truth. Each appears to have arisen from a recognition of certain more or less unconsciously selected and uncritically interpreted phenomena by each of several men

who secured different facts and attempted explanations.

In a few animals the "germ plasm" may be morphologically early differentiated and reasonably continuous, though governed by the same laws as other tissues. In others, any part of the general tissues may give rise to a complete organism. The behavior of some organisms is intelligent and purposeful, while that of others is largely mechanical. Some structural responses of sessile organisms are advantageous, some indifferent and some harmful. Some of the more fixed structures of the highly individuated animals are advantageous, some indifferent, and some disadvantageous (Metcalf, '13). No other type of general statement appears to be tenable, yet each extreme of each proposition has at some time or other been the subject of some all-inclusive doctrine.

Such are the limitations of an individual's knowledge and the psychic limitations of our race and generation. In considering the psychology of religion, Ames ('10, p. 394) points out similar well-recognizable tendencies in that field of human activity and quotes Cooley on social development as follows:

> Much energy has been wasted or nearly wasted, in the exclusive and intolerant advocacy of special schemes—single tax, prohibition, state socialism and the like, each of which was imagined by its adherents to be the key of millennial conditions. Every year makes converts to the truth that no isolated scheme can be a good scheme, and that real progress must be advanced all along the line.

Advance all along the line is what biological science must achieve. This I believe means the encouraging of all lines of indirect attack, whether they at first throw light on the ideal central question of pure science or important practical problems or not. It means the exercising of extreme caution in the application of criteria of values to scientific results. Such measures tend not only to stifle the best initiative in good investigators, but also tend to check the building up of fruitful hypotheses. The latter danger is greatest in connection with the mechanistic criterion referred to above. As has already been stated, criteria of values can be safely applied only

as broad general guides, and investigation should be measured on the basis of its thoroughness, the originality shown, etc.

In science special schemes of course do not exist recognized as such, but intolerant application of criteria of values results in essentially the same condition. One often hears the statement made by so-called scientific men, that this or that line of investigation has been pursued for several years, but has failed to yield important advances or generalizations, but they add, we will be very glad to recognize it as soon as its value is proven. This seems to us to be a distinctly unscientific attitude, and but a polite modern statement of a spirit which in former generations often sent men to the stake or dungeon. This is true because to these polite objectors its value is rarely or never proven. It is "schemes" (preconceived theories) thus presented that have in the recent past stifled the study of responses by discouraging efforts in that direction and thus contributed materially toward making zoology the unorganized science which it is to-day. We must recognize that the various aspects of zoology pure and applied have never been well correlated, less so we believe than in any other branch of natural science, clearly less than in botany. In general, animal physiology has been isolated in medical schools and genetics, faunistics and morphology have not been properly influenced by it, while morphologists for many years held themselves aloof from other workers.

In a discussion dealing mainly with the doctrine of natural selection in the origination of adaptations, Mathews ('13) has sounded the keynote of a growing attitude toward all response questions. Out of the infinite different combinations which may enter into the proteid molecule and the varying rates at which metabolic action may go forward, innumerable types of irritability and correlated structure have been and still are arising under the influence of environment external and internal. Of these some are incompatible with life, others indiffer-

ent, and others advantageous. Upon these physiological characters natural selection has operated to eliminate, and with time has perhaps rendered of less frequent occurrence, those characters that are incompatible with their conditions of existence. External form, color ornamentation, etc., while no doubt often of importance themselves are more often the advantageous or indifferent correlatives of physiological or irritability types which are compatible with their conditions of existence. The study of irritability and response may be pursued in many ways—by experiment, by observation in nature alone or combined with experiment. The mapping of stimulating conditions in nature, of the distribution of types of irritability and response, which is one function of field ecology and modern geography, can hardly fail to contribute materially to the advance of knowledge in many lines, including that of the physico-chemical mechanism of life. The student of experimental ecology has an infinite field of problems and methods thrown open to him by the organization of such information relative to responses. Still in our attempt to make advances along the line of the study of responses, we must not forget that it is but one of several lines of advance, all of which must sooner or later be correlated with a view to broader generalization.

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AN APTEROUS DROSOPHILA AND ITS GENETIC BEHAVIOR

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AMONG the various mutants of the fruit-fly, *Drosophila ampelophila,* which have arisen from cultures in this laboratory, is one entirely destitute of wings, and hence called *apterous*.[1] The study of the heredity of this form has been difficult because of its almost complete (apparent) sterility. In order, therefore, to determine to which of the three groups of linked characters of *Drosophila* it belonged I was obliged, in most crosses, to make use of heterozygous flies that carried the factor for apterous. As this process is unique in certain regards, it will be described in some detail.

METHODS OF STUDY

At first it was thought that the apterous mutant was completely sterile, since none of the first flies, as they appeared occasionally in certain cultures, could be crossed even with normal individuals. At last, however, offspring were obtained from an apterous female by a wild male, and a permanent line started. But this line could not be perpetuated by means of apterous individuals, for these were unable to breed.[2] It had, therefore, to be kept up by means of heterozygous, winged flies. The method was as follows: The original cross of winged by apterous gave in F_2 approximately 3 winged to 1 apterous. Of the winged class approximately two thirds were heterozygous for apterous, and when mated together gave the same

[1] This apterous fly is quite distinct from that called wingless in earlier papers by Morgan, and now known as vestigial.

[2] Only twice, aside from the original mating, were apterous individuals successfully crossed, and then only to winged specimens, never to their own kind. These two cases are given in experiments II and III.

3 : 1 ratio. Selecting again from the winged flies, the process could be repeated indefinitely. The only difficulty lay in the fact that no visible character differentiated the heterozygous from homozygous winged flies, and consequently all matings had to be made in pairs taken at random, with the result that about 56 per cent. of the cultures were rendered worthless. In actual practise large numbers were mated in pairs, and then all discarded save those producing apterous.[3] This was the method used in keeping up stock.

To obtain the necessary combination of apterous with other mutant factors, winged offspring from apterous-throwing parents were mated in pairs to flies of the desired stock. One third of the normals from apterous stock were pure for the normal allelomorph of apterous and rendered worthless all matings in which they were involved; but the other two thirds were heterozygous for apterous, and when crossed with the desired stock gave in F_2 some apterous offspring. If the F_1 flies were bred *en masse,* approximately 15 winged to 1 apterous were obtained, but if bred in pairs, certain pairs (those in which both members were heterozygous for apterous) gave 3 winged to 1 apterous. The latter method was the one actually used in most cases. In this manner the same end result was attained as would have been secured by using apterous individuals in crosses with other stocks, the only difference being in the amount of labor involved in making up a larger number of cultures. Both kinds of crosses were, in fact, used, as will be seen below.

The use of symbols in this paper follows the system recently adopted by Morgan and other students of *Drosophila* (Morgan, 1913, *a* and *b*). That is, for any pair of allelomorphic characters a capital letter is used to indicate the dominant, and a small letter the recessive factor—the symbol being taken from the name of the mutant. Since the apterous character is recessive, the symbols for the

[3] In the fourth experiment a character (black) was introduced which differentiated homozygous from heterozygous and thus made it possible to pick out the heterozygous individuals.

apterous fly become a_p–a_p, and those for the winged fly A_p–A_p. In other words, A_p is a factor in the wild fly necessary for wing production, while a_p is its modified homologue responsible for lack of wings in the mutant. The apparent contradiction in using A_p, not for the factor responsible for apterous, but for its normal allelomorph, may be confusing at first sight, but a little familiarity with the system obviates this difficulty.

Experiments

Experiment I.—Long-winged, red-eyed ♂ by apterous, white-eyed ♀ (from miniature wing stock).

F_1 All winged. Long-winged, red-eyed females.
Miniature winged, white-eyed males.

F_2 Winged and apterous as follows:

Winged:
- Long-winged, red-eyed males and females.
- Long-winged, white-eyed males and females.
- Miniature-winged, red-eyed males and females.
- Miniature-winged, white-eyed males and females.

Apterous:
- Apterous, red-eyed males and females.
- Apterous, white-eyed males and females.

This experiment shows the inheritance of the apterous character to be Mendelian, giving in F_1 all winged, and in F_2 approximately 3 winged to 1 apterous. Table I contains a summary of the offspring from 21 pairs of the F_1 and F_2 individuals, giving a total of 1,405 winged to 450 apterous,—a ratio of 3.12 to 1.

The absence of apterous flies in F_1 indicates at once that the apterous character is not sex-linked. The presence of miniature-winged flies in F_1 and F_2 indicates that the apterous factor is independent of the miniature-wing factor, which latter must have been carried by the apterous female (coming from miniature wing stock), and transmitted to her offspring unaffected by the apterous factor.

Analysis of the cross:

A_p, factor necessary for wing production. a_p, its allelomorph, in the apterous fly.

M, factor necessary for the production of long wings (sex-linked).

m, allelomorph of M responsible for miniature wings.

W, factor necessary for the production of eye color (sex-linked).

w, allelomorph of W responsible for white eyes.

P_1	Long, red male	$A_pMWX\text{–}A_p$,
	Apterous, white female	$a_pmwX\text{–}a_pmwX$.
F_1	Long red females	$A_pMWX\text{–}a_pmwX$,
	Miniature white males	$A_p\text{–}a_pmwX$.

F_2, leaving out of account the sex-linked factors and considering only winged vs. apterous:

Gametes of F_1 A_p, a_p.
A_p, a_p.

F_2

Winged $\begin{cases} A_p\text{–}a_p. \\ A_p\text{–}A_p. \\ A_p\text{–}a_p. \end{cases}$

Apterous $a_p\text{–}a_p$.

Experiment II.—Long vermilion ♀ by apterous, white ♂.[4] This cross is practically the reciprocal of Exp. I, except that vermilion replaces red eye color in the winged parent. Like Experiment I it involves two pairs of sex-linked characters, aside from the apterous character. The results are essentially like those of Experiment I and may be passed over briefly.

P_1	Long, vermilion ♀	$A_pMWX\text{–}A_pMWX$,
	Apterous, white ♂	$a_pmwX\text{–}a_p$.[4]

[4] The white-eyed, apterous ♂ in this cross is white-vermilion, *i. e.*, the double recessive, and therefore when crossed with vermilion it gives vermilion instead of red in F_1.

F_1 Long, vermilion ♀ A_pMWX–a_pmwX,
Long, vermilion ♂ A_pMWX–a_p.

F_2 Long vermilion ♀ and ♂
Long, white ♂
Miniature, vermilion ♂
Miniature, white ♂
} Winged.

Apterous, vermilion ♀ and ♂
Apterous, white ♂
} Apterous.

TABLE I

Offspring from Pairs Heterozygous for Apterous in Experiment I. Parents taken from F_1, F_2 and F_3

Mating No.	Winged	Apterous	Ratio
41	122	32	3.8 : 1
53	41	14	2.9 : 1
56	29	12	2.5 : 1
64	46	30	1.5 : 1
65	29	16	1.8 : 1
80	85	28	3.04: 1
83	71	20	3.5 : 1
84	13	3	4.3 : 1
85	40	9	4.4 : 1
111	183	64	2.8 : 1
112	20	10	2 : 1
117	99	42	2.4 : 1
118	28	10	2.8 : 1
130	32	7	4.5 : 1
131	76	26	3.1 : 1
132	71	19	3.7 : 1
134	92	36	2.6 : 1
151	58	12	4.8 : 1
170	78	10	7.8 : 1
171	63	15	4.5 : 1
177	129	35	3.6 : 1
	1,405	450	

Average ratio of winged to apterous, 3.12:1.

An analysis of the F_2 is not essential here and is omitted for the sake of brevity. It may be derived from the F_1 formulæ. Table II indicates the expected classes and ratios in F_2 and gives the actual numbers obtained in culture No. 59, in which each class was recorded separately. In subsequent cultures of this experiment no attempt was made to separate any but the winged and apterous classes. Counts of the latter are given in Table III.

TABLE II

MATING 59

F_2—Expected Classes	Expected Ratio	Actual Ratio	Actual No.
Long verm. ♀	12	13.8 : 1	185
Long verm. ♂	3	4.2 : 1	57
Long white ♂	3	2.4 : 1	31
Miniature verm. ♂	3	2 : 1	26
Miniature white ♂	3	4 : 1	53
Apterous verm. ♀	4	3.2 : 1	44
Apterous verm. ♂	2	1.2 : 1	15
Apterous white ♂	2	2 : 1	24

TABLE III

F_2 FROM MASS CULTURES

Culture No.	Winged	Apterous	Ratio
58	367	78	4.7 : 1
59	352	83	4.2 : 1
96	556	114	4.8 : 1
97	306	70	4.3 : 1
120	597	103	5.08: 1
135	554	104	5.3 : 1
137	405	49	8 : 1
154	298	45	6.6 : 1
157	405	53	7.6 : 1
	3,840	699	Average ratio, 5.5 : 1.

F_2 FROM PAIRS

Culture No.	Winged	Apterous	Ratio
155	141	35	4.1 : 1
156	38	11	3.4 : 1
	179	46	Average ratio, 3.9 : 1.

F_3 FROM PAIRS

Culture No.	Winged	Apterous	Ratio
160	119	25	4.7 : 1
162	123	27	4.6 : 1
172	266	62	4.3 : 1
173	87	26	3.4 : 1
174	165	37	4.5 : 1
175	167	42	4 : 1
176	171	46	3.7 : 1
177	129	35	3.6 : 1
178	92	23	4 : 1
	1,319	323	Average ratio, 4.08: 1
	179	46	
	1,319	323	
Total from pairs,	1,498	369	Ratio, 4.6 : 1.

It will be noted that the apterous classes fall a little below the expected numbers in most cases. This is characteristic of all weak races of *Drosophila*, and is doubtless due to the inability of some flies to mature. Of the winged classes the first two and the fifth exceed the Mendelian ratios, while the other two fall short, due to linkage between white, vermilion and miniature.[5] The distribution of apterous, however, is entirely independent of the others, showing that the factor responsible for it is not a member of the group containing those responsible for vermilion eyes, white eyes, or miniature wings.

The ratio of winged to apterous in this particular culture is 4.2:1. Table III includes a summary of this and nineteen similar cultures in which the parents were all descendants of the long-winged, vermilion-eyed female by the apterous male mentioned above. The first nine are mass cultures, the next two are pairs, from F_1 flies. Below these are offspring from nine pairs of F_2 flies.

It is noticeable that the ratio of apterous to winged is greater in cultures where pairs are used than in mass cultures, though all parents in the latter are heterozygous. This, I believe, is unquestionably due to the low viability of the apterous flies, which prevents some of them from maturing in cultures where the competition is severe. For this reason the averages are given separately for pairs and for mass cultures. The average from pairs is 4.06:1, while that from mass cultures is 5.5:1. This low viability is also shown by pairs, if the food conditions are not good, or if the culture becomes very dry.

Experiment III.—To determine the relation between apterous and characters in Group III.

It is obvious from Experiments I and II that apterous is not a sex-linked character (Group I). The present experiment is for the purpose of determining its relation to characters of Group III. As a representative of the latter group pink eye color was chosen. The results of the cross between this and apterous may be passed over briefly

[5] For discussion of linkage between these characters see Morgan, 1911.

since they are similar to previous results in showing no linkage. A winged, pink-eyed male bred to an apterous, vermilion-eyed female (from Experiment III) gave, as expected, winged, vermilion-eyed males and winged, red-eyed females in F_1. These inbred gave four classes of winged and four classes of apterous, *i. e.*, red, vermilion, pink and orange.[6] The ratios are such as to show independent segregation of apterous and pink. Below is a summary of the expected and actual results.

P_1	Apterous, vermilion ♀	$a_p v P X - a_p v P X$,
	Winged, pink ♂	$A_p V p X - A_p p$.
F_1	All winged. Red ♀	$a_p v P X - A_p V_p X$,
	Verm. ♂	$a_p v P X - A_p p$.

Eight kinds of eggs and four kinds of spermatozoa are formed by these F_1 flies, giving, through random fertilization, 32 classes of offspring divided into eight groups, as shown in Table IV.

TABLE IV

F_2 Expected Results			Actual Results in Experiments						
Classes	Ratio		627		628[7]	629	630	631	Total
Winged, red	9	9	85	143	34	120	35	70	402
Winged, vermilion	9		58						
Winged, pink	3	3	25	35	3	38	11	24	111
Winged, orange	3		10						
Apterous, red	3	3	22	35	15	32	11	21	114
Apterous, vermilion	3		13						
Apterous, pink	1	1	7	15	0	10	2	7	34
Apterous, orange	1		8						

In the table red and vermilion have been considered together as one class, because they both contain *P;* and similarly pink and orange have been considered together because they both contain *p*. The total numbers for the four classes give the ratios 402 : 111 : 114 : 34, or 10.8 : 3.6 : 3.35 : 1,—a sufficiently close approximation to the expected

[6] Orange eye is the double recessive *pv–pv*.

[7] In this culture the ratios are seen to diverge widely from the expected, due, I believe, to the poor cultural conditions in this case which prevented some of the weaker pink and orange flies from maturing

9:3:3:1. These results clearly show the independence (*i. e.,* lack of linkage) of apterous and pink.

Table V includes all matings (giving apterous) in Experiment III, for the purpose of showing the ratio of winged to apterous.

TABLE V

Mating No.	Winged	Apterous	Ratio
627	178	50	3.56 : 1
628	37	15	2.47 : 1
629	158	42	3.7 : 1
630	46	13	3.53 : 1
631	94	28	3.36 : 1
646	48	10	4.8 : 1
649	81	27	3.1 : 1
650	44	14	3.15 : 1
651	124	37	3.35 : 1
652	92	34	2.7 : 1
674	50	19	2.63 : 1
692	75	27	3.15 . 1
	1,027	316	

Average ratio winged to apterous, 3.25:1.

Experiment IV.—To determine the relation between apterous and characters in Group II.

The mutant called "black" (having black body and wings) was used in this experiment as a representative of Group II. No direct matings with apterous individuals, such as obtained in the three preceding cases, could be effected here, and consequently the winged brothers and sisters of apterous had to be used for crossing with black, according to the method described in the introduction. Matings of this kind (in pairs) gave, in F_1, winged flies, some of which were heterozygous for apterous and black. These inbred (also in pairs) gave winged and apterous, and gray and black, as shown below:

P_1 Black ♂ homozygous for wings A_pb–A_pb,
Gray ♀ heterozygous for apterous A_pB–a_pB.

F_1 Winged, heterozygous for black A_pb–A_pB,
Winged, heterozygous for black and apterous A_pb–a_pB.

Only pairs in which both members were of the second type (A_pb–a_pB,—heterozygous for apterous) could pro-

duce apterous. The others, therefore, are ignored. Considering the second type alone, the analysis becomes:

F_1 gametes (expected) A_pb–A_pB–a_pb–a_pB,
A_pb–A_pB–a_pb–a_pB.

F_2 Expected classes.

a_pB–a_pB	apterous, gray.
a_pB–a_pb	apterous (heterozygous for black).
a_pB–A_pB	winged, gray.
a_pB–A_pb	winged, heterozygous for black.
a_pb–a_pB	apterous, heterozygous for black.
a_pb–a_pb	apterous, black.
a_pb–A_pB	winged, heterozygous for black.
a_pb–A_pb	winged, black.
A_pB–a_pB	winged, gray.
A_pB–a_pb	winged, heterozygous for black.
A_pB–A_pB	winged, gray.
A_pB–A_pb	winged, heterozygous for black.
A_pb–a_pB	do.
A_pb–a_pb	winged, black.
A_pb–A_pB	winged, heterozygous for black.
A_pb–A_pb	winged, black.

Expected ratios: 3 winged black; 6 winged heterozygous for black; 3 winged gray; 1 apterous black; 2 apterous heterozygous for black; 1 apterous gray.

Actual results: winged black, winged heterozygous for black, and apterous gray, as shown in Table VI.

In the last two matings black and heterozygous offspring were counted as one class.

Total: winged 701; apterous 174 or 4.02:1.

The expectation for the F_2 if A_p and B segregate independently is equal numbers of black and gray among the winged and among the apterous offspring. Actually, however, the apterous flies are all gray, and the winged flies are all black or heterozygous for black. Furthermore, the

ratio of heterozygotes to pure blacks in the winged class shows that the flies which should have been gray according to expectation have been added to the heterozygotes. Likewise the gray flies in the apterous class are about four times as numerous as anticipated, showing that the expected heterozygotes and blacks are here gray. From this it is evident that the factors a_p and B, on the one hand, and A_p and b, on the other, have remained associated in the combination which they formed in the parents, instead of independently segregating. Such an explanation accounts for the absence of A_pB and a_pb gametes in the F_1 generation, and consequently for the absence of gray, winged flies, and of black or heterozygous apterous flies in F_2. The evidence accords with that obtained for many other mutant characters in *Drosophila,* and the explanation is the same as that given for the previous cases (*e. g.*, Morgan, 1911, 1912; Morgan and Lynch; Sturtevant, 1913 *a* and *b;* Dexter).

TABLE VI

ACTUAL RESULTS

Mating No.	Winged			Apterous		
	Gray	Black	Heterozygous	Gray	Black	Heterozygous
703	0	15	52	18	0	0
724	0	22	71	26	0	0
732	0	20	54	15	0	0
733	0	29	59	15	0	0
741	0	19	50	19	0	0
745	0	35	86	30	0	0
746	0	15	42	13	0	0
		155	414	136		
725		53		14		
734		79		24		

The presence of a definite linkage or association between apterous and black (*i. e.*, between either a_p or A_p and b or B depending upon the nature of the cross) as shown by this experiment, together with the absence of any such linkage with characters in Groups I and III, as shown by the preceding experiments, indicate that apter-

ous is a member of Group II and is, presumably, associated or linked with all other characters belonging to that group.

Supposedly this association of the characters results from an association of the factors responsible for them in the germ cells. And this latter association has been explained upon the assumption that factors responsible for linked characters are located in the same chromosome. The hypothesis has even been carried so far as to postulate a linear arrangement of the factors within the chromosome—the relative position of the factors being determined by the degree or amount of linkage existing between them. This conception and the data upon which it is based have been amplified by Morgan and by Sturtevant, and need not be dwelt on here. In the present case no attempt has been made to ascertain the exact degree of linkage between apterous and other characters in the group, except black, because of the difficulty of breeding the apterous flies. Apparently the linkage between apterous and black is very close, if not complete, since no case of "crossing over" was observed among the 875 F_2 offspring in this experiment (Table VI). There is a possibility that the classification of the F_2 apterous flies as all gray is not absolutely correct, because, owing to the difficulty of distinguishing gray from heterozygous black in apterous specimens, an occasional heterozygous fly might have passed for pure gray. However, if there had been any appreciable number of cross-overs in this direction, there would also have been some in the opposite direction, which fact would have been indicated by the presence of winged, gray flies. And since none of these were observed, it is safe to conclude that few or no cross-overs occurred, and hence that apterous is very closely, if not completely, linked to black.

Experiment V.—To determine the relation between the apterous mutant and the "vestigial" mutant.

Among the mutant characters of Group II is one called "vestigial wing." Flies having this character are more

like the apterous individuals than are any of the other mutants, and since the two characters belong to the same group the question arose as to whether or not the factor responsible for one might be simply a modification of that responsible for the other. Experiment V was performed to determine this point.

Long-winged flies heterozygous for apterous were crossed with vestigial winged individuals, and F_1 and F_2 generations raised. The F_1 flies were all long winged, which fact in itself indicates the independence of the two characters, for if they were allelomorphs either apterous or vestigial should have appeared. In F_2 both vestigial and apterous, as well as long-winged, flies appeared, showing conclusively the independence of the two characters.

Summary of Experiments

Experiments I and II show that the apterous character is a simple Mendelian recessive, which independently mendelizes with miniature wings, white eyes and vermilion eyes, and hence is not sex-linked (*i. e.*, not a member of Group I).

Experiment III shows that the apterous factor is transmitted independently of the factor for pink eye, thus indicating that apterous is not a member of Group III.

Experiment IV shows a linkage ratio to result from crosses involving apterous and black, the ratio being such as to indicate a very close linkage between apterous and black, and to identify apterous as a member of Group II.

Experiment V shows apterous to be distinct from vestigial wing, to which it bears a considerable degree of resemblance.

Origin and Characteristics of the Apterous Mutant

The description of the apterous fly has been deferred up to this point in order that it might be combined with a discussion of the experimental results.

The mutant has appeared upon several occasions, but

always in the same stock (miniature white), and always with the same evidence of weakness and low viability. Fig. 1 is a camera drawing of a typical specimen, made by Miss E. M. Wallace. In morphological characters the fly differs from the normal in being entirely destitute of wings and in possessing greatly reduced balancers. Likewise in physiological characters it deviates strikingly from the normal.

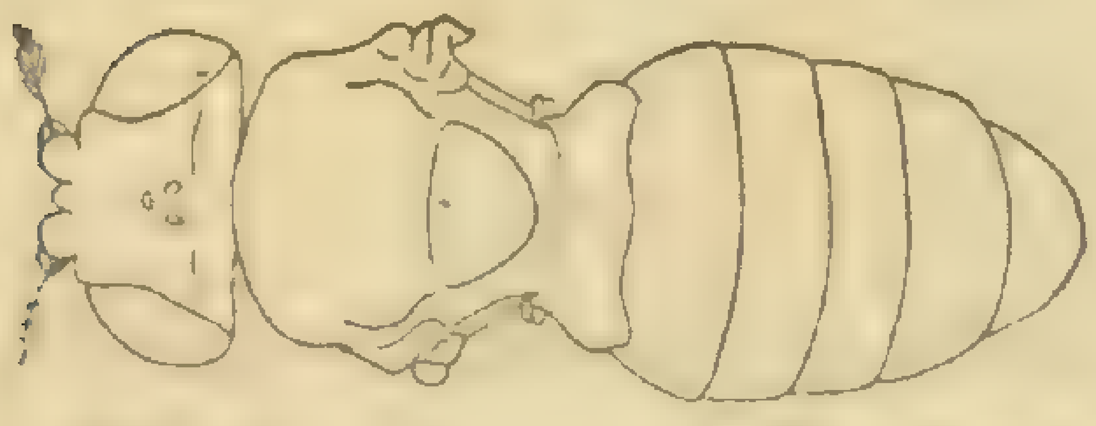

FIG. 1. APTEROUS MUTANT OF *Drosophila ampelophila.*

This is best shown by means of a comparison between apterous flies and normal flies from which the wings have been removed. The latter are not appreciably inconvenienced by their loss of wings; they show characteristic vigor in their active running and jumping movements, they easily right themselves if overturned, or extricate themselves if entangled in food or cotton, and they are long lived and breed as prolifically as do winged individuals. In fact they show no ill effects except the inability to fly. The true apterous individuals, on the other hand, show marked abnormalities in all these respects. Instead of being vigorous and active they are weak and usually sluggish; if overturned they have great difficulty in righting themselves; or, if entangled in food or cotton, they are usually unable to extricate themselves and consequently perish. Moreover, they are always short lived, even when kept under the best possible conditions and prevented from becoming entangled in food or cotton. And lastly they exhibit a most marked inability to breed, as noted in the experiments. This characteristic, as has been mentioned above, is so marked that the apterous flies were at first thought to be sterile. I am convinced now, however, that the difficulty is not one of sterility at all, but is due to a physical weakness which makes it extremely difficult for the flies to copulate, and for the females, even when fertilized, to produce and lay eggs. Cytological examination has shown that the males produce spermatozoa in an apparently normal manner, yet prolonged observation of

the flies has not revealed a single copulation or attempt at copulation on the part of an apterous male.[8] Similarly the females have been shown to produce rudimentary eggs in an apparently normal manner, and in two cases females have produced offspring when fertilized by winged males, thus indicating their fertility. But many other cases have been observed in which apterous females were fertilized by winged males (or at least in which copulation took place), and yet in these observed cases the females invariably died without producing offspring,[9] because, I believe, of their physical weakness.

From these facts it appears practically certain that the apparent sterility is not due to infertility of either sperm or eggs, but results from a weakness which makes it very difficult for the apterous flies to perform the reproductive processes.

This explains why no crosses have been secured between apterous and apterous, although each sex has been successfully crossed to winged. It is also supported by the fact that from the cross between apterous male and winged female a large number of offspring were secured, since the winged female could produce many eggs,—whereas in the two crosses between apterous females and winged males only a very few offspring were secured. because the apterous females could only produce a few eggs.

When the experiments were first begun it was hoped that sooner or later one or more inherently vigorous apterous flies would appear which might give rise to a vigorous race. But nothing of the sort took place, although numbers of the apterous flies were given opportunity to breed all through the course of the experiments. Obviously, then, the physiological characteristics, as

[8] Copulation in normal flies can be observed with very little difficulty. It is evident that at least one case of copulation by an apterous male occurred, namely in Experiment II.

[9] Judging from the cases observed a large number (probably one hundred or more) of apterous females must have been fertilized by winged males during the course of these experiments, yet only three of these gave progeny.

shown by vigor and viability, are directly associated with morphological characters and are not to be separated from them by selection. In other words, the "factor" responsible for lack of wings is also responsible for physiological disturbances.

The only suggestion of an inherent difference between different races, or strains of apterous, is the slight difference in the percentage of apterous offspring in Experiments I and III as compared with II and IV. In I and III the ratios of winged to apterous are 3.12:1 and 3.24:1, respectively, while in Experiments II and IV they are 4.06:1 and 4.02:1. This deviation is not great, but it is fairly constant, and is sufficient, I believe, to indicate a real difference. But whether it is to be explained upon the assumption that in I and III the apterous parents were inherently stronger than in II and IV is not so clear. It might equally well be explained upon the basis of differences in the winged races to which apterous was crossed. Unfortunately, an experimental analysis of the question is prohibited by the difficulty of breeding the apterous flies, and it must, therefore, be left open. One fact, however, is clear, namely that there is no progressive increase in viability of the apterous flies, for the apterous parent in Experiment II, where the viability appears to be low, was descended directly from that in I where it appears to be high, and likewise the parent from the apterous side in IV was obtained directly from III.

In conclusion it may be profitable to call to mind briefly the bearing of certain of the above data on the question of the nature and behavior of Mendelian "factors."

The present case of a definite correlation between lack of wings, reduction in size of balancers, and weak physical constitution in the apterous race of *Drosophila*, shows clearly that one factor may have far reaching effects, and not be limited to any particular part or organ,—a fact

which has been long known, and often mentioned,[10] but by no means universally recognized.

Correlated with, or resulting from this principle is the conception that the final result of ontogenetic development is not due to the *independent* action of various factors and their products, but is due to the *combined* action, or the *interaction* of these products during development. To illustrate by the wing of a fly,—it is probable that the normal development of such an organ is not dependent solely upon one factor, but that it is influenced by many factors. This is strongly suggested by data derived from the various wing mutations in *Drosophila*. These have dealt with a large number of factors, each of which is responsible for a definite wing modification. For instance, one factor is responsible for miniature wings, another for vestigial, another for rudimentary, another for curved, etc.[11] From the fact that these mutant factors (which may be considered as modifications of factors in the normal fly) influence the wings, it seems highly probable that their normal allelomorphs also influence wing production in the wild fly.

Finally I wish to thank Dr. T. H. Morgan for kindly assistance and advice in connection with this work.

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[10] Most recently, perhaps, by Morgan (1913*a*, page 9): "A change in a factor may have far-reaching consequences. Every part of the organism capable of reacting to the new change is affected. Though we seize upon the most conspicuous difference between the old type and its mutant, and make use of this alone, every student of heredity is familiar with cases where more than the part taken as the index is affected. Weismann's theory, on the other hand, seems to identify each character with a special determinant . . ."

[11] The same is true for various eye colors, and body colors.

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SHORTER ARTICLES AND DISCUSSION

FORMULÆ FOR THE RESULTS OF INBREEDING

In connection with Pearl's recent valuable analyses of the results of inbreeding (1, 2, 3), a comparison of these results with those from self-fertilization is of interest. In my note on the latter (4), I gave a formula for the rate at which organisms become homozygotic through continued self-fertilization. This occurs more slowly in the various types of inbreeding, but Pearl gives no general formula for it. For purposes of comparison I have worked out from Pearl's data the general formula for the rate at which organisms become homozygotic through continued brother by sister mating; as such formulæ appear to be of permanent value, it is here given.[1] What the formula gives is, precisely, (1) the proportion of individuals that will be homozygotic for any given character after any number of unbroken generations of such inbreeding, (2) the average proportion of the characters of a given individual that will be homozygotic after any number of unbroken generations of such inbreeding. The numerical value so obtained may conveniently be called the coefficient of homozygosis.

The formula turns out to be a combination of the successive powers of 2, with the successive terms of the Fibonacci series, which appears in so curious a way in various natural phenomena. In this series every term is the sum of the two preceding terms, the series beginning: 0, 1, 1, 2, 3, 5, 8, 13, etc.

Let $x =$ the coefficient of homozygosis.

$n =$ the number of inbred generations (the number of times successive brother by sister mating has occurred).

f_1, f_2, f_3, etc., $=$ the successive terms of the Fibonacci series (thus $f_1 = 0$, $f_2 = 1$, etc.).

Then the formula for the coefficient of homozygosis is:

$$x = \frac{2^{n-1} + f_1 \cdot 2^{n-2} + f_2 \cdot 2^{n-3} \ldots \text{etc.}}{2^n}$$

(The terms in the numerator are continued until the exponent of 2 becomes 0.)

[1] In conversation, Dr. Pearl urged the publication of the present note, otherwise I should not at this time have dealt with a matter which he has under analysis.

Thus, if the number of inbreedings (n) is 1.

$$x = \frac{2^0}{2^1} = 1/2, \text{ or } 50 \text{ per cent.}$$

If $n = 4$

$$x = \frac{2^3 + 0.2^2 + 1.2^1 + 1.2^0}{2^4} = 11/16, \text{ or } 68.75 \text{ per cent.}$$

If $n = 9$

$$x = \frac{2^8 + 0.2^7 + 1.2^6 + 1.2^5 + 2.2^4 + 3.2^3 + 5.2^2 + 8.2^1 + 13.2^0}{2^9}$$

$$= 457/512, \text{ or } 89.26 \text{ per cent.}$$

If $n = 16$

$$x = \frac{63819}{65536} \text{ or } 97.38 \text{ per cent.}$$

As these examples show, the formula gives the results that were obtained by Pearl in the detailed working out (so far as this was carried), as given in Pearl's table I (2, p. 62). (It will be noted that Pearl counts as generation *1* the one *before* inbreeding has occurred, so that his generation 10, for example, is that in which there have been 9 inbreedings ($n = 9$).)

If one is working out the values of the coefficient x for a series of generations, the above formula may be expressed as a simple rule, applicable after the value for $n = 1$ is obtained. This rule is:

The value of the coefficient of homozygosis x for any term (as the nth) is obtained by doubling the numerator and denominator of the fraction expressing the value for the previous term, and adding to the numerator the corresponding ($n - 1th$) term of the Fibonacci series.

Or, in view of the peculiar nature of the Fibonacci series, the rule may be expressed as follows:

Double the numerator and denominator, and add to the numerator the sum of the last two numbers so added.

Thus, since

x for 1 inbreeding $= 1/2$

x " 2 " $= \frac{2 \times 1 + 0}{2 \times 2} = 2/4$

x " 3 " $= \frac{2 \times 2 + 1}{2 \times 4} = 5/8$

x " 4 " $= \frac{2 \times 5 + 1}{2 \times 8} = 11/16$, etc.

After obtaining x, or the proportion of homozygotes for any one pair of characters, the proportion y for any number m of pairs is obtained simply by raising x to the mth power, that is:

$$y = x^m.$$

Thus, after two generations of brother × sister mating, the proportion of homozygotes for three pairs of characters is $(1/2)^3 = 1/8$, or 12.5 per cent. After 8 generations of such inbreeding the proportion homozygotic for 10 pairs of characters is:

$$\left(\frac{222}{256}\right)^{10} = 24.05 \text{ per cent.}$$

The corresponding value in the case of continued self-fertilization is 99.61 per cent. (4, p. 491).

Whether it may be possible to obtain a similar formula for the coefficient of homozygosis in the cases of mating of cousin × cousin or of parent × offspring, remains to be discovered.

Pearl's "coefficient of inbreeding" gives the percentage of *lacking* ancestors in a given pedigree, as compared with the number that would be present if all the parents were unrelated. In order to compare self-fertilization with inbreeding in this respect, Pearl's formulæ for the coefficient of inbreeding may be expressed in terms of the number of successive inbreedings (n); for many purposes the formulæ appear more convenient so expressed. The following gives these formulæ for self-fertilization and the three types of inbreeding, together with those, so far as worked out, for the proportion of individuals homozygotic with respect to a given character. In all these, n is the number of successive self-fertilizations or inbreedings.

	Coefficient of Inbreeding.	Coefficient of Homozygosis.
Self-fertilization	$\frac{2^n - 1}{2^n}$	$\frac{2^n - 1}{2^n}$
Brother × Sister	$\frac{2^n - 2}{2^n}$	$\frac{2^{n-1} + f_1 \cdot 2^{n-2} + f_2 \cdot 2^{n-3} \cdots \text{etc.}}{2^n}$
Cousin × Cousin	$\frac{2^{n-1} - 2}{2^n}$	?
Parent × Offspring	$\frac{2^n - n - 1}{2^n}$	?

It will be observed that in self-fertilization the value of the coefficient of inbreeding is, curiously, the same as that of the coefficient of homozygosis, while in the other cases there is no evident simple relation between the two. Further, the coefficient

of inbreeding in brother × sister mating is the same as for self-fertilization, save that it lags one generation behind the latter; thus the coefficient for the fourth generation of self-fertilization is the same as that for the fifth of brother × sister mating. Pearl (1, p. 592) has already pointed out that in cousin mating the coefficient is one-half that for brother × sister, with a lag of one generation; as compared with self-fertilization the lag is two generations. No such simple relation is apparent between the proportions of homozygotes resulting from the diverse methods of breeding, though possibly such may yet be discovered.

H. S. JENNINGS

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A SHORT-CUT IN THE COMPUTATION OF CERTAIN PROBABLE ERRORS

IN his handbook of statistical methods, on p. 38, Dr. C. B. Davenport[1] gives a short method for the calculation of the probable errors of some of the commonest statistical constants, in a table of logarithmic formulæ. It would seem that the simple and obvious short-cut involved has not been given the attention it deserves in connection with non-logarithmic calculation. The logarithmic formulæ are as follows:[2]

$$(1)\quad \log E_A = \log .6745 + \log \sigma - \tfrac{1}{2} \log n \left[\text{since } E_A = .6745 \frac{\sigma}{\sqrt{n}}\right],$$

$$(2)\quad \log E_\sigma = \log E_A - \tfrac{1}{2} \log 2 \left[\text{since } E_\sigma = .6745 \frac{\sigma}{\sqrt{2n}}, \text{ or, } E_\sigma = E_A \div \sqrt{2}\right],$$

[1] Davenport, C. B., "Statistical Methods with Special Reference to Biological Variation," 2d ed., 1904, New York, John Wiley & Sons.

[2] *A* indicates the weighted arithmetic mean, σ the standard deviation, and *C* the coefficient of variability.

(3)[3] $\log E_C = \log E_\sigma - \log A$ [since $E_C = E_\sigma \div A$].

Now, if one is working with a calculating machine, he can simply carry the value of E_A to two or three more decimal places than are to be retained, and then divide by the square root of 2 to get E_σ; similarly, the latter value, divided by the mean, gives E_C.

The writer prefers, however, to calculate the values in the ordinary way on the machine, using Miss Gibson's[4] table for $\frac{.6745}{\sqrt{n}}$ and $\frac{.6745}{\sqrt{2n}}$, and then to use the short method in checking. The original computations can be indicated and performed with great confidence and rapidity, since it is hardly possible to make an error that will not be discovered in the checking.[5] It is obviously safer, as well as much quicker, to check in this way than to repeat the original processes.

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GALTON AND DISCONTINUITY IN VARIATION

It seems not to be generally realized that Galton recognized both continuity and discontinuity, both in variation and inheritance. Of course, all biologists are familiar with "Galton's polygon," in which slight oscillations of the polygon on one of its faces, but without a change of face, are compared with "small unstable deviations" (fluctuations), while a larger oscillation, in which the polygon moves over to a new face, is compared to a

> sport . . . of such marked peculiarity and stability as to rank as a new type, capable of becoming the origin of a new race with very little assistance on the part of natural selection.[1]

Galton's polygon illustrated for him how the following conditions may co-exist:

> (1) Variability within narrow limits without prejudice to the purity of the breed. (2) Partly stable sub-types. (3) Tendency, when much disturbed, to revert from a sub-type to an earlier form. (4) Occasional sports which may give rise to new types.

These four types would seem to correspond rather well to what

[3] Formula (3) gives, of course, the approximate or uncorrected value of E_C.

[4] Gibson, Winifred, "Tables for Facilitating the Computation of Probable Errors," *Biometrika*, 4: 385–393. 3 tables.

[5] Unless, of course, one misreads the figures from the machine in checking.

[1] "Natural Inheritance," London, 1889, p. 28.

are now called (1) fluctuations or "non-inherited" (in reality, I think, partially inherited) continuous variations; (2) instability resulting from a heterozygous or partially heterozygous condition; (3) reversions, now believed to result chiefly from crossing; and (4) mutations.

Galton is equally explicit in other statements on this subject. Like Darwin, he admitted the facts both of continuity and discontinuity in variation; but, unlike Darwin, he also recognized discontinuity or alternation as well as continuity or blending, in inheritance. Thus he says, in a paragraph headed "stability of sports":[2]

> Experience does not show that those wide varieties which are called "sports" are unstable. On the contrary, they are often transmitted to successive generations with curious persistence. Neither is there any reason for expecting otherwise. While we can well understand that a strained modification of a type would not be so stable as one that approximates more nearly to the typical center, the variety may be so wide that it falls into different conditions of stability, and ceases to be a strained modification of the original type.

In another paragraph,[3] headed "Evolution not by minute steps only," he says:

> The theory of evolution might dispense with a restriction, for which it is difficult to see either the need or the justification, namely, that the course of evolution always proceeds by steps that are severally minute, and that become effective only through accumulation. That the steps *may* be small and that they *must* be small are very different views; it is only to the latter that I object. . . . An apparent ground for the common belief is founded on the fact that wherever search is made for intermediate forms between widely divergent varieties, whether they be of plants or of animals, of weapons or utensils, of customs, religion or language, or of any other product of evolution, a long and orderly series can usually be made out, each member of which differs in an almost imperceptible degree from the adjacent specimens. But it does not at all follow because these intermediate forms have been found to exist, that they are the very stages that were passed through in the course of evolution. Counter evidence exists in abundance, not only of the appearance of considerable sports, but of their remarkable stability in hereditary transmission.

Again, Galton not only believed in the existence of both blended and alternative inheritance, but he recognized the im-

[2] *L. c.*, p. 30.
[3] *L. c.*, p. 32.

portance of the latter in connection with the survival of new races. Thus he writes:[4]

> The quadroon child of the mulatto and the white has a quarter tint; some of the children may be altogether darker or lighter than the rest, but they are not piebald.[5] Skin-color is therefore a good example of what I call blended inheritance. . . .
>
> Next as regards heritages that come altogether from one progenitor to the exclusion of the rest. Eye-color is a fairly good illustration of this. . . .
>
> There are probably no heritages that perfectly blend or that absolutely exclude one another, but all heritages have a tendency in one or the other direction, and the tendency is often a very strong one.

On the following page Galton remarks that

> A peculiar interest attaches itself to mutually exclusive heritages, owing to the aid they must afford to the establishment of incipient races.

He thus recognizes the invalidity of Darwin's objection to "single variations" as a factor in evolution, namely, that they would certainly be swamped by crossing with the general population.

It would, therefore, appear that in his recognition of continuity as well as discontinuity both in variation and heredity, Galton was in advance of his time, and more in accord with some of the current views.

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REPULSION IN MICE

In the February number of the American Naturalist Dr. C. Little criticizes the results of my mouse-breeding experiments which I published in the *Zeitschrift für Induktive Abstammungs- und Vererbungs-lehre* Bd. VI, Heft 3. The chief point, on which he disagrees with me, is the interpretation of the results I obtained in breeding black and albino mice together.

The fact is, that in my paper on mice, I overlooked a serious error. In three sentences on page 126, relating to test matings of albinos, the words "black" and "agouti" changed places. As printed in the paper these sentences run:

> Without exception they have given *black* or equal numbers of *black* and albino young, depending upon the purity of the black used. But never has one of these albinos produced a single *agouti* young in a mating with black. Counting together the colored young of such families I get 89 *black* young.

[4] *L. c.*, p. 12.

[5] Cases of piebaldism in such crosses are of course now well-known.

These errors were corrected in an "errata" in Band VI, heft 5, which Dr. Little unhappily did not find. The sentences should read:

Without exception they have given *agouti,* or equal numbers of *agouti* and albino young, depending upon the purity of the black used. But never has one of these albinos produced a single *black* young in a mating with black. Counting together the colored young of such families I get 89 *agouti* young.

Professor Punnett was so kind as to draw my attention to these mistakes. They were corrected in the reprints sent out.

The facts were simply these: Albinos were bred of two sorts, with and without G (the gene which agoutis have more than blacks). These albinos can only be distinguished by test-mating them to blacks. The albinos with G (aG) give agouti young, if mated to black (Ag), the ag albinos give black young from such a mating. In one series, some agoutis were produced, which were heterozygous for A as well as for $G(AaGg)$. Ordinarily, such agoutis, when mated inter se, produce 9 agouti (1 $AAGG$, 2 $AAGg$, 2 $AaGG$, 4 $AaGg$), 3 black (1 $aaGG$, 2 $aaGg$) and 4 albinos (1 $aaGG$, 2 $aaGg$, 1 $aagg$) in every sixteen. Mated to albinos without $G(ag)$ the ordinary $AaGg$ animals give four kinds of young, agoutis ($AaGg$), blacks ($Aagg$) and two kinds of albinos ($aaGg$) and ($aagg$) in equal numbers.

Now these particular $AaGg$ animals did not produce four kinds of gametes, as expected, namely, AG, Ag, aG and ag, but only two kinds, Ag and aG. Thirty one agoutis were test-mated to $aagg$ albinos. These test matings gave 181 young, of which 94 were black ($Aagg$) and 87 albino ($aaGg$). No agoutis were produced.

As a further proof, the result of breeding these agoutis inter se can be adduced. These matings gave 73 agouti ($AaGg$), 37 black ($AAgg$) and 32 albinos ($aaGG$). Of these 32 albinos, thirteen were tested by mating them to blacks. If one of them should have lacked G, it would have given black young. But no black young were produced. Some young were albino (when the black parent was heterozygous for A), but all the colored young were agouti (89 in all).

This, I hope, will make it perfectly clear, that in this series we have been dealing with a case of repulsion between the genes A and G.

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THE OSTEOLOGY OF A DOUBLE-HEADED CALF

THROUGH the kindness of Mr. Charles O. Reed, taxidermist, of Fairmont, W. Va., the writer received the skulls and anterior cervical vertebræ of a double-headed calf which seemed of sufficient interest to warrant a brief description.

According to Mr. Reed the calf's mother was a four-year-old, thoroughbred Herford, living at Grafton, W. Va., owner not mentioned.

At her first labor this cow gave birth to twins, supposedly normal, though it was not so stated. The second calf was "slightly deformed," but in what way Reed did not know. The third labor produced the double-headed calf in question, which was of unusual size, and was killed in parturition. According to Reed "This calf would have lived if it could have been brought through O. K." He dissected it and found the "alimentary canal, blood vessels and trachea normal."

The bones in the occipital region are slightly broken, probably done in disarticulating the skulls from the neck; and in the left skull the left premaxilla was lost and was replaced by a roughly carved piece of wood for the sake of symmetry.

In macerating the skulls, for the purpose of removing all the flesh, many of the loose sutures separated, and in gluing the bones together again it was not always possible to completely close the sutures.

As may be seen in the figures there is a considerable though not very great difference in the size of the skulls, the right being the larger. They were detached from the cervical vertebræ when received, but the photographs show their approximate position in relation to the neck and to each other.

Each skull is twisted and bent away from the other, the bend being most marked just cephalad to the orbits. The left skull is the more distorted.

The articulation of the skulls with the fused atlas was so crude that Reed, who had seen the skulls before disarticulation, had to be appealed to to decide which skull was right and which was left.

Fig. 1 is a photograph of the dorsal aspect of the skulls and the first three cervical vertebræ. The distortion of the two skulls is of about the same character but is, as noted above, more marked in the left skull.

The parietal (*p*) is normal. The posterior regions of the frontals (*f*) are normal, but their anterior ends are bent laterally,

which causes a slight curvature in the sagittal suture. It is in the region of the lachrymals (l) that the distortion is most marked, so that the lachrymal on the convex side of the bend, especially

Fig. 1. Dorsal Views of the Two Skulls and of the First Three Cervical Vertebræ. Mandibles in Position.

a, atlas; *ax*, axis; *e*, extra bone between maxilla and premaxilla; *f*, frontal; *l*, lachrymal; *m*, malar; *mx*, maxilla; *n*, nasal; *o*, occipital; *p*, parietal; *pm*, premaxilla.

in the left skull, is much longer than that on the opposite side; the same is true of the malars (*m*), of the maxillaries (*mx*), and, to a less degree, of the premaxillæ (*pm*). The nasals (*n*) are also unsymmetrical, but do not differ much in size; they are simply, as a pair, pushed to the side.

Fig. 2. The ventral aspect of the skull shows even greater abnormalities than the dorsal. The occipital (*o*), as noted above, was somewhat injured by the person who disarticulated the skulls from the neck, but it is quite unsymmetrical, especially in its exoccipital region. In the left skull (right in this figure) all the other bones seen in this aspect are bent, but in the other skull most of the bones are comparatively straight.

In the right skull a suture in front of the teeth separates off an extra bone (*e*) on each side, between the maxilla and the premaxilla, that of the right side being much the larger. In the left skull these extra bones are not present though a partial suture,

extending about half way through the left maxilla, is visible in this view of the skull.

FIG. 2. VENTRAL VIEWS OF THE SKULLS AND THE FIRST TWO CERVICAL VERTEBRÆ. MANDIBLES REMOVED.

Fig. 3 shows the curious distortion of the mandibles, which seem to be bent in more or less the same direction. In the right mandible the left half has four incisor teeth, the right half has three. In the left mandible the right half has four teeth, the left half has three, though one tooth is missing from each half.

As noted above, the skulls, when received, were disconnected from the vertebræ; but the latter, three in number, were strung together on a small piece of rope and presumably were the first three cervicals; they are shown in a dorsal view in Fig. 1, ventral view in Fig. 2, and anterior view in Fig. 3. The first of these is presumably a compound atlas (*a*) since it articulates with each of the skulls, though in a very crude way. It consists of eight loosely united elements which became completely separated in cleaning and had to be glued together again. In the dorsal view, Fig. 1, is seen a small, irregular bone from which radiate three somewhat symmetrical bones, the largest lying in the median plane between the bases of the skulls. This larger

bone is pierced by two large foramina; each of the other two bones shows in this view a foramen which branches and opens both on the antero-median and the postero-lateral surfaces. The

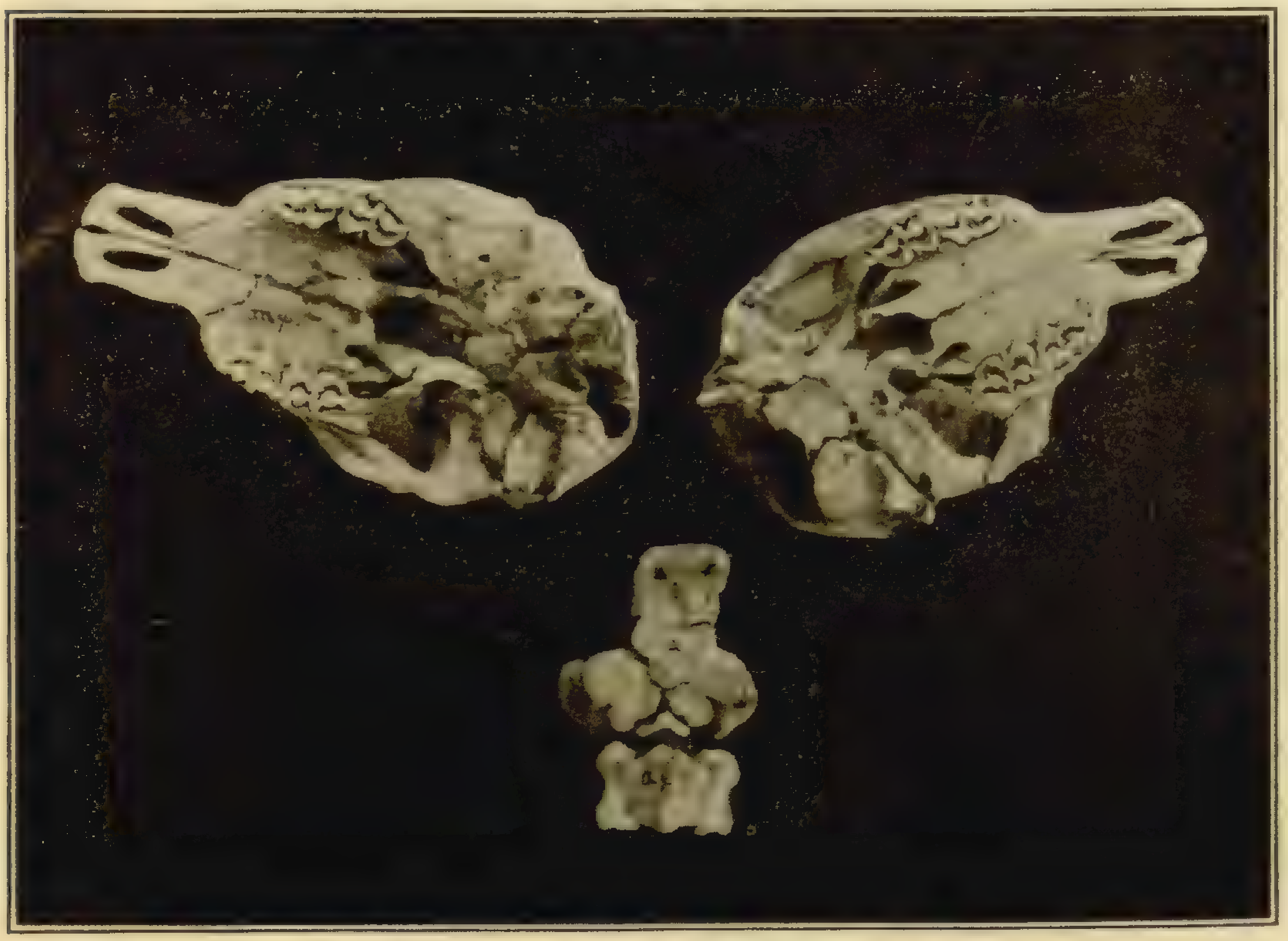

FIG. 3. DORSAL VIEWS OF THE MANDIBLES AND ANTERIOR VIEWS OF THE FIRST THREE CERVICAL VERTEBRÆ.

ventral view, Fig. 2, shows a very irregular group of bones, the smallest of which is for articulation with the following vertebra.

The second vertebra (*ax*), supposedly the axis, exhibits no indication of an odontoid process and articulates in a very crude way with the preceding bone. Its dorsal spine is rather elongated in an antero-posterior direction, but otherwise it bears no closer resemblance to an axis than to any other cervical vertebra. Its centrum was so loosely fused with the arch on either side it became detached in cleaning and had to be glued in place.

The third vertebra exhibits no peculiarities that warrant description.

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THE FAILURE OF ETHER TO PRODUCE MUTATIONS IN DROSOPHILA

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THE many mutants of *Drosophila ampelophila* that have appeared "under domestication" have raised the question as to the cause or causes that have brought about the result. Since every fly that has passed through our hands has been *etherized* once in its life, usually before it begins to lay its eggs if a female or before mating if a male, it might appear that this recurring condition was responsible for the mutations. At any rate it seemed worth while to put this view to a test, if for no other reason than to remove from one's mind the suspicion that ether "did it."

Preliminary trials showed that two drops of ether (on a piece of cotton) in a quart milk bottle, tightly stoppered with a cotton plug, would not noticeably affect the flies in half an hour, three drops made them slightly "stupid," four drops more so, and five drops quieted them. It was found that they would for the most part recover even after 6, 7 and 8 drops of ether. If etherized twice daily the flies were so far weakened that they generally died without laying any eggs. Therefore in the later experiments the flies were etherized only once a day or once in two days.

The larvæ (beginning two days after the eggs were laid,

at which time the eggs have hatched) can stand more ether. Twice daily throughout their larval and pupal lives (approximately 11 days) 6, or 7, or 8, or 9 or even 10 drops of ether were added to the quart bottles. The ether excited the larvæ at first, then quieted them; later they recovered. In such tests the larvæ were kept almost continuously in an atmosphere of ether from birth to emergence of the fly and in a few cases the etherization was continued with the flies also. By covering a wide range of stages and conditions I hoped to find the critical point, if any such existed, when ether would act. Since, as the sequel will show, no specific results were obtained it seems unnecessary to give the details of all these trials.

Double, and in one case triple recessive, stocks were used for the work, because experience had already shown that even with great care contamination may occur. One or two flies that came from escaped mutants would ruin the value of the data, but the operator can protect himself by using stocks that have already two or more recessive characters. If such flies mutate in one of the characters involved the presence of the other one will make it certain that the mutant belonged to this culture, and had not come in from outside; if a change appeared in some other part, the double recessive character would still identify the stock. Two of the stocks used had sex-linked characters, *i. e.,* eosin miniature and cherry club vermilion. If a mutation should appear that involved these characters it would become evident at once in the male offspring; for, the male gets his single sex chromosome from his mother and exhibits her sex-linked factors. Of course this would be equally true for any other sex-linked character that appeared, but in practise it is impossible to thoroughly examine each fly in every possible part, so that I had to confine my attention to certain organs, and in these cases I concentrated on the mutant characters. Conspicuous mutations in other parts would, I think, have been picked up, but minor ones would probably have been missed. On the other hand, if changes taking place in

the chromosomal material are the basis for mutation it would seem perhaps a priori unlikely that the same changes should occur at the same time in both members of a pair, and if not the effect would not appear in the next generation, and not until two flies of the later progeny each carrying one mutant factor met. Whatever weight may be attached to this argument—we know really nothing as to the origin of mutations—it seemed necessary to carry some stocks to another generation; and this was done.

The following are the totals of offspring produced by flies from larvæ that had been etherized twice daily from the time of hatching to the winged state:

Black vestigial	310 556
Pink black	1,390
Eosin miniature	871
Cherry club vermilion	364
Pink ebony sepia	1,311
Total	4,802

In the next case fewer drops of ether were used—four or five throughout larval and pupal life. The parent flies were changed to new bottles quite often to prevent crowding and abundant food was supplied:

Black vestigial	2,122
Pink black	6,762
Eosin miniature	2,603
Pink ebony sepia	953
Total	12,440

The following data are from the offspring of the flies that had 8 and 10 drops of ether twice daily:

Pink black	3,440
Eosin miniature	2,775
Total	6,215

The next data are the records of the offspring of

adult flies that had been etherized several times (usually twice a day) just after they had hatched:

Black vestigial (6 times)	870
Black vestigial (7 times)	143
Black vestigial (8 times)	694
Pure black (6 times)	81
Eosin miniature (3 times)	206
Eosin miniature (5 times)	428
Cherry club vermillion (8 times)	713
Cherry club vermillion (8 times)	476
Total	3,611

Finally some of the flies that had appeared, in the experiments in which 8 and 10 drops of ether had been used throughout the larval and pupal life, were bred and gave in the next generation the following records:

Pink black	2,186
Eosin miniature	666
Cherry club vermillion	709
Pink ebony sepia	539
Total	4,100

In a grand total of 31,168 flies subjected to ether, there was not a single mutation observed. It seems highly probable therefore that ether has no specific effect in producing mutations in *Drosophila ampelophila*. It might, of course, still be said that mutations are so rare, that, although caused by ether, they still are not frequently enough produced to make 31,000 flies a sufficient guarantee. Granting this, it still remains that since no mutants appeared under this excessive treatment, ether does not play the rôle of a specific agent causing the mutations of *Drosophila*, and one is inclined to look elsewhere for a solution of the problem.

One of the first mutants that I observed in *ampelophila* appeared in the offspring of flies that had been treated with radium and although there was no proof that the radium had had a specific effect I felt obliged to state the actual case, refraining carefully from any statement of

causal connection.[1] Nevertheless, I have been quoted as having produced the first mutants by the use of radium. I may add that repetition of the experiment on a large scale both with the emanations of an X-ray machine and from radium salts has failed to produce any mutations, although the flies were made sterile for a time. Loeb and Bancroft also tried the effect of radium.[2] They found a black mutant type after treatment with radium but since the same type appeared in the control they do not believe that its appearance had any connection with the radium. They also state that after treatment a white-eyed female appeared in the first generation, and suggest that a white eyed male may have existed in a previous generation that escaped notice, but if it had been found in a previous generation, the mutation or the contamination must have been earlier than the one that produced the white-eyed female; for, a white-eyed male takes two generations to reappear again. Pink-eyed flies were also found both in the control and in the treated flies. In regard to another mutant type, they state:

> We succeeded in producing short winged specimens in two different cultures by treating them with radium, while thus far we have not observed this mutation in cultures not treated with radium.

But although "two hundred different cultures" were subsequently treated with radium and no short-winged (miniature) flies appeared, I get the impression that Bancroft and Loeb must have had stock that was already contaminated by some recessive mutant factors. All of these mutants had been obtained and described by us, and the stock used by Bancroft and Loeb was obtained in part at least from my friend Dr. Frank E. Lutz, who had at that time in his possession, as a letter I have from him states, certainly two of these mutants, black and miniature, that he had received from me. It seems to me not improbable that the collector, who got the stock from Dr.

[1] *Science*, XXXIII, 1911.

[2] *Loc. cit.*

Lutz for Professor Loeb, included by mistake some flies heterozygous for these two characters; for in our very extensive experience with wild stock from Cold Spring Harbor (the origin of most of Dr. Lutz's stock) and elsewhere these mutants have never arisen again.

At various times experiments have been made in this laboratory involving wide ranges of temperature,[3] salts, sugars, acids, alkalis without any resulting mutation. In fact, our experience with *Drosophila* has given us the impression that mutations are rare events, although the actual number of our mutants is now quite large.

Guyénot[4] also has treated *ampelophila* to high temperatures, to radium and to X-rays without result. When the adult flies were treated with ultra-violet light, however, a definite type of "black" fly was obtained. The first eggs that such females lay are normal and give rise to normal flies. The eggs laid later fail to hatch, although they appear to begin their development. On the third day amongst the abnormal eggs some were found that gave rise to flies that were apparently normal. It happened that they were not examined again until after the flies of the next generation had appeared (many of them had died). Both among the living and the dead flies there was a considerable percentage of black flies. The black females laid eggs which did not develop, even although normal males were added. Why the black males were not also tested by outcrossing is not apparent. The description of the black flies given by Guyénot tallies in some points with our stock of ebony in which the females were at first usually infertile but the males fertile. At first, indeed, we kept the stock by breeding the ebony males to the heterozygous females. These are intermediate in color. In fact, Guyénot seems to have had heterozygous flies but did not, according to his account, obtain any black flies from them. However, if the ultra-violet light is a specific agent for these mutations the experiment can easily be repeated.

[3] *Science*, XXII, 1910.

[4] *Bull. Scientifique*, XLVIII, 1914.

It should be added that only one of Guyénot's two lines gave dark flies after treatment with ultra-violet light. This might seem to indicate that the first result was accidental, or due to the presence of a recessive mutation in the stock prior to treatment were it not that a careful control is recorded. Guyénot himself speaks with much caution concerning the interpretation of his results. Decision as to their value may be reserved until repetition of the experiment gives confirmation. Our own experience with *Drosophila* shows that mutations appear under conditions where all the other flies in the same culture are normal and we have become unduly sceptical perhaps towards evidence which refers a particular mutant to some unusual treatment to which the flies have been subjected. Until we can get definite information as to how mutants arise, whether through external influences, through accidents of mitosis, through hybridizing, or through changes in the chromosomes with its consequent dislocations of the machinery of crossing over, or in some other way, it seems futile to discuss the question.

THE ANALYSIS OF A CASE OF CONTINUOUS VARIATION IN DROSOPHILA BY A STUDY OF ITS LINKAGE RELATIONS

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OLIVET COLLEGE

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I. INTRODUCTION

HARDLY had the principles of Mendelism been worked out in one species of plant than apparent exceptions to these principles were discovered. Mendel's own case of the breeding true of species hybrids in *Hieracium* was the first of these, and since 1900 others have been reported.

Further analysis has shown that many of these early cases are readily interpreted on Mendelian principles, while for other exceptions, like that of *Hieracium*, for instance, the true explanation has been found without in any way coming into conflict with Mendelism.

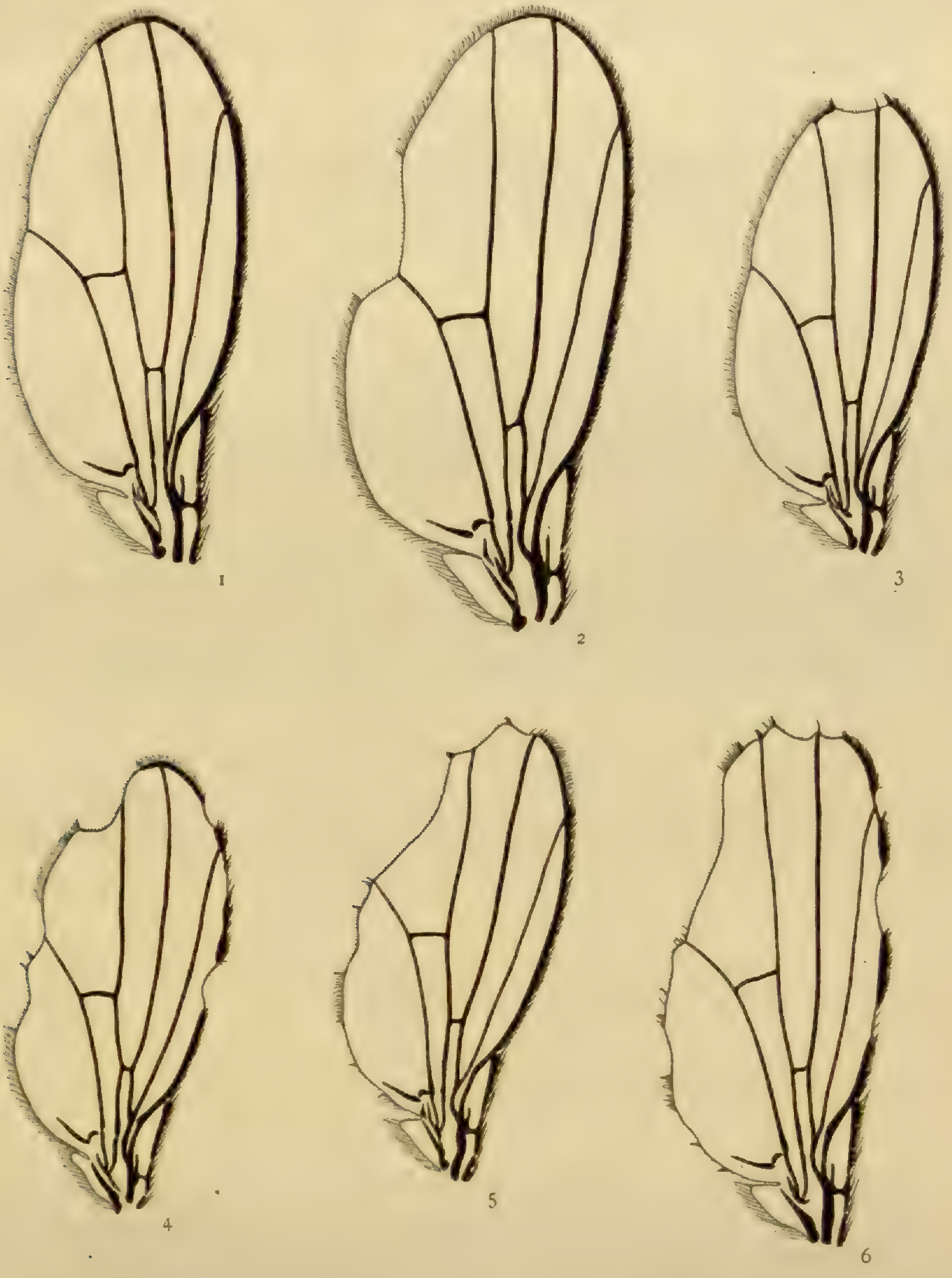
The masking of a Mendelian ratio may be effected in many ways, and some of the most important of the recent work in genetics has dealt with this problem. Among the conditions so far brought to light may be mentioned the following:

(*a*) *Multiple Factors.*—Recent papers by MacDowell (1914) and Shull (1914) have discussed at length the literature and history of this subject. In brief, the work that has been done shows that in both animals and plants the production of certain characters is brought about through the action of two or more independently Mendelizing pairs of genes that have similar effects on the developing organism. If the effect of these genes is cumulative, so that the character is more or less produced according to the number of dominant genes present, the type of inheritance known as blended inheritance is produced. If the effect is not cumulative, the recessive character does not appear with the frequency of 1:3, but with the frequency of 1:15, 1:63, etc., according to the number of pairs of genes concerned.

(*b*) *The Effect of the Environment.*—A typical case of this sort is reported by Baur (1912). In crossing a dark red to a red strain of *Antirrhinum*, a complete series between the red and the dark red appeared in the F_2 generation; the effect of light on the plants was such that plants that had developed in a bright light had a darker color than those that had developed in a less intense light. The analysis of the F_3 generation, however, proved conclusively that one fourth of the F_2 plants had been homozygous dark reds, one fourth had been homozygous red, and two fourths had been heterozygotes. Morgan (1912*a*) has described a case in *Drosophila* in which moisture conditions in the bottle in which the flies are developing determine to a certain extent whether or not certain

characters shall appear; and Hoge (1914) has shown that certain temperatures are necessary for the development of reduplicated legs in *Drosophila*. Other examples may be found in the literature of genetics.

(*c*) *Lethal Characters.*—There have been reported several instances in recent years of animals and plants which are unable to live if homozygous for certain genes. The



case of yellow mice, Baur's *Aurea*-strain of *Antirrhinum* (Baur, 1912) and the modified sex-ratios in *Drosophila* reported by Morgan (1912*d*) are examples of this phenomenon.

The object of the present paper is to describe a case of inheritance in *Drosophila* that for some years seemed to

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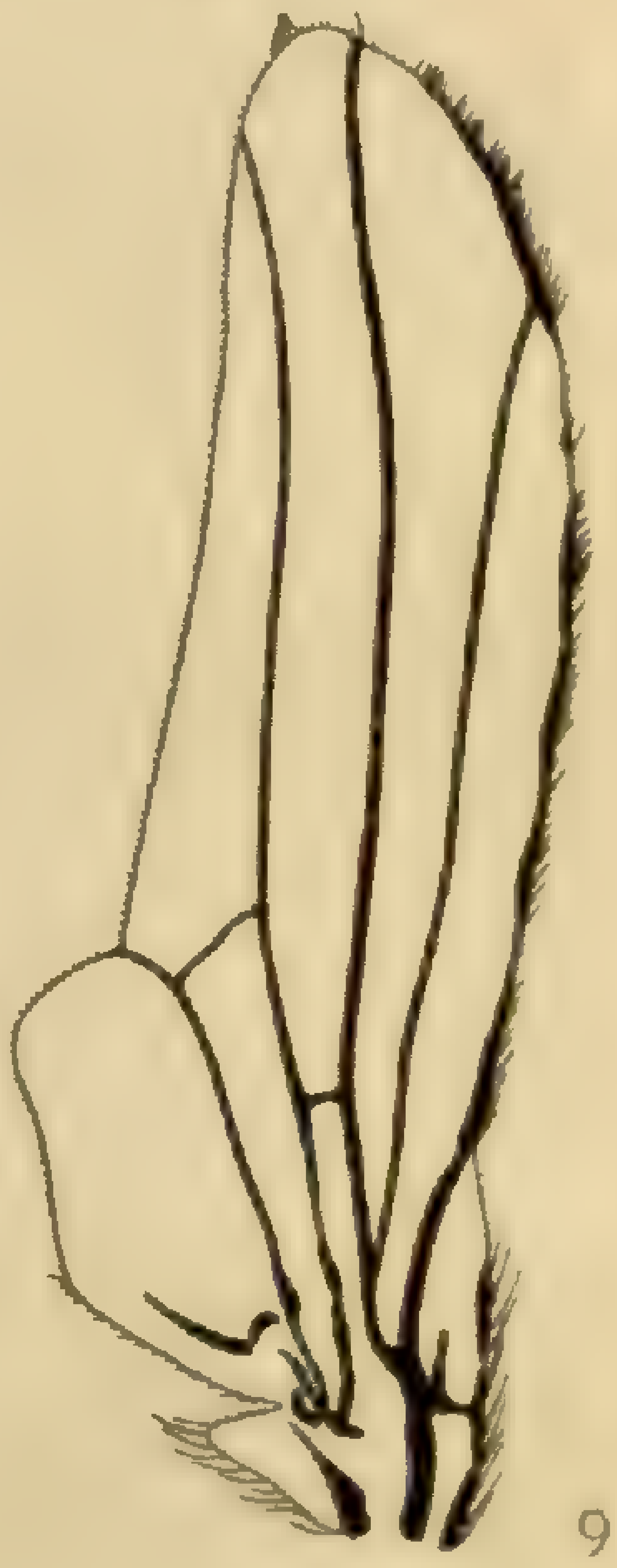
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defy Mendelian analysis. Though all the details of the case have not been worked out, enough has been done to show that it is brought about by factors which segregate in the ordinary Mendelian fashion, and that the difficulties which it still presents are not opposed to that hypothesis.

The case under consideration is that of Beaded wings, which, according to Morgan (1911*a*), first appeared in May, 1910, among flies that had been exposed during part of their early life to radium rays.

The appearance of these wings can best be understood from the figures (Figs. 1–12), which represent a few of the forms that may appear in a stock culture. All gradations may be found between wings perfectly normal and mere strips, such as shown by Figure 11.

In the early days of its history, according to Morgan, the Beaded-winged flies did not breed true, but for many generations produced many normal-winged offspring. At the time when I took up the experiment, however, the stock bred almost 100 per cent. pure; that is, almost every fly hatched had wings more or less Beaded. I have at present a strain which breeds true, throwing only Beaded-winged offspring, and most of the offspring have the Beading in an extreme form. Most of my work has been done with this stock.

II. THE GERMINAL CONSTITUTION OF BEADED FLIES

A. Crosses between Beaded and Wild Flies

1. *Behavior in First Generation*

When a Beaded fly is mated to a normal fly of a normal Wild stock, a considerable number of flies with Beaded wings usually appears in the first generation (F_1). The percentage is not constant, but varies between zero and about fifty per cent. (See Table I.) From Chart 1, it appears possible that the average percentage of Beaded-winged offspring per pair is near 10–15 per cent. or else near 30–35 per cent. of the total offspring. The exact

average is 25.5 per cent. That there is a bimodal curve produced may perhaps not be significant, as will appear

TABLE I

Crosses of Beaded to Wild Flies, showing Percentages of Beaded-winged Offspring

	Per Cent. of Flies with Beaded Wings										
	0–4.9	5–9.9	10–14.9	15–19.9	20–24.9	25–29.9	30–34.9	35–39.9	40–44.9	45–49.9	50–100
Number of broods giving this percentage	1	5	10	6	7	7	14	3	2	2	2
Average size of brood	203	172	148	120	180	113	101	95	130	50	73

from the following facts, although later evidence will show that it very possibly is significant.

The per cent. of Beaded-winged offspring given by one pair (Beaded × Wild) may vary at different times and

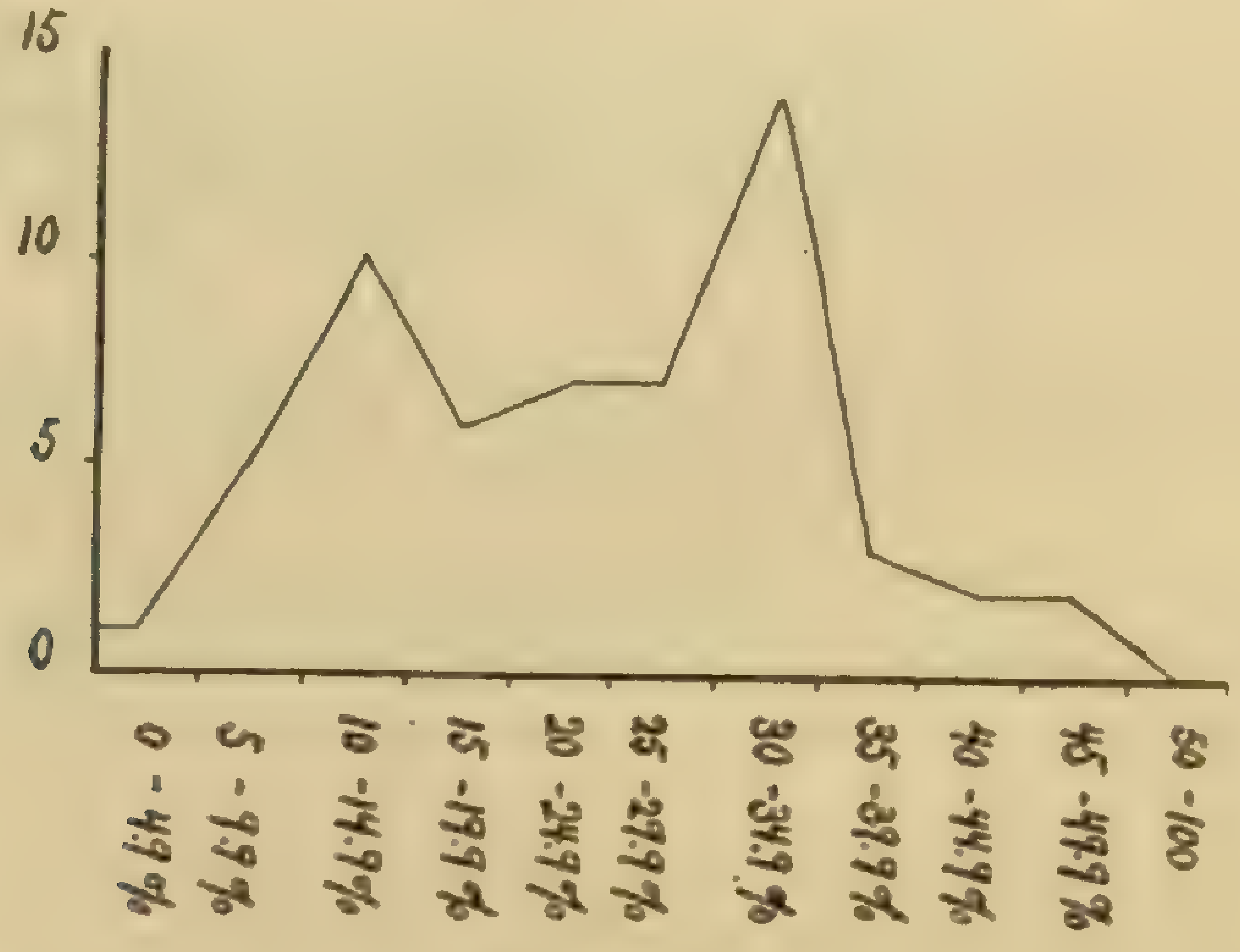


Chart I

Numbers of broods giving certain percentages of Beaded-winged offspring in F_1 generation of Beaded × Wild. (See Table I).

under different conditions. For instance, if a pair are put into a bottle with food and are left there for ten days, and are then put into another bottle with fresh food and left another ten days, the percentage of Beaded-winged offspring will be different in the two broods. Table II gives the records of such tests. The first two were made

with single pairs. In the third case, a Beaded male was given four virgin females, so that although all the offspring have the same father, they come from four mothers. Inspection of this table shows that it is quite impossible to assign the parents of any one brood to any definite class based on the percentage of Beaded-winged offspring that they give.

TABLE II

DIFFERENT PERCENTAGES OF BEADED-WINGED OFFSPRING BY THE SAME PARENTS DURING TWO SEPARATE TEN-DAY PERIODS IN DIFFERENT BOTTLES

	First Ten Days		Second Ten Days	
	No. of Offspring	Per Cent. Beaded	No. of Offspring	Per Cent. Beaded
First pair	126	21	179	41
Second pair	117	7	146	22
One father ×4 mothers	389	20	301	28

Table II shows also that the parents gave a larger percentage of Beaded-winged offspring during the second ten days than during the first period. That this is a coincidence appears from Table III. Here it is shown from the records of fifty broods chosen at random, that

TABLE III

PERCENTAGES OF BEADED-WINGED FLIES IN THE FIRST COUNT OF A BROOD COMPARED WITH THOSE OF THE LAST COUNT (INTERVAL OF FROM EIGHT TO TEN DAYS). BASED ON COUNTS FROM FIFTY BROODS, CHOSEN AT RANDOM

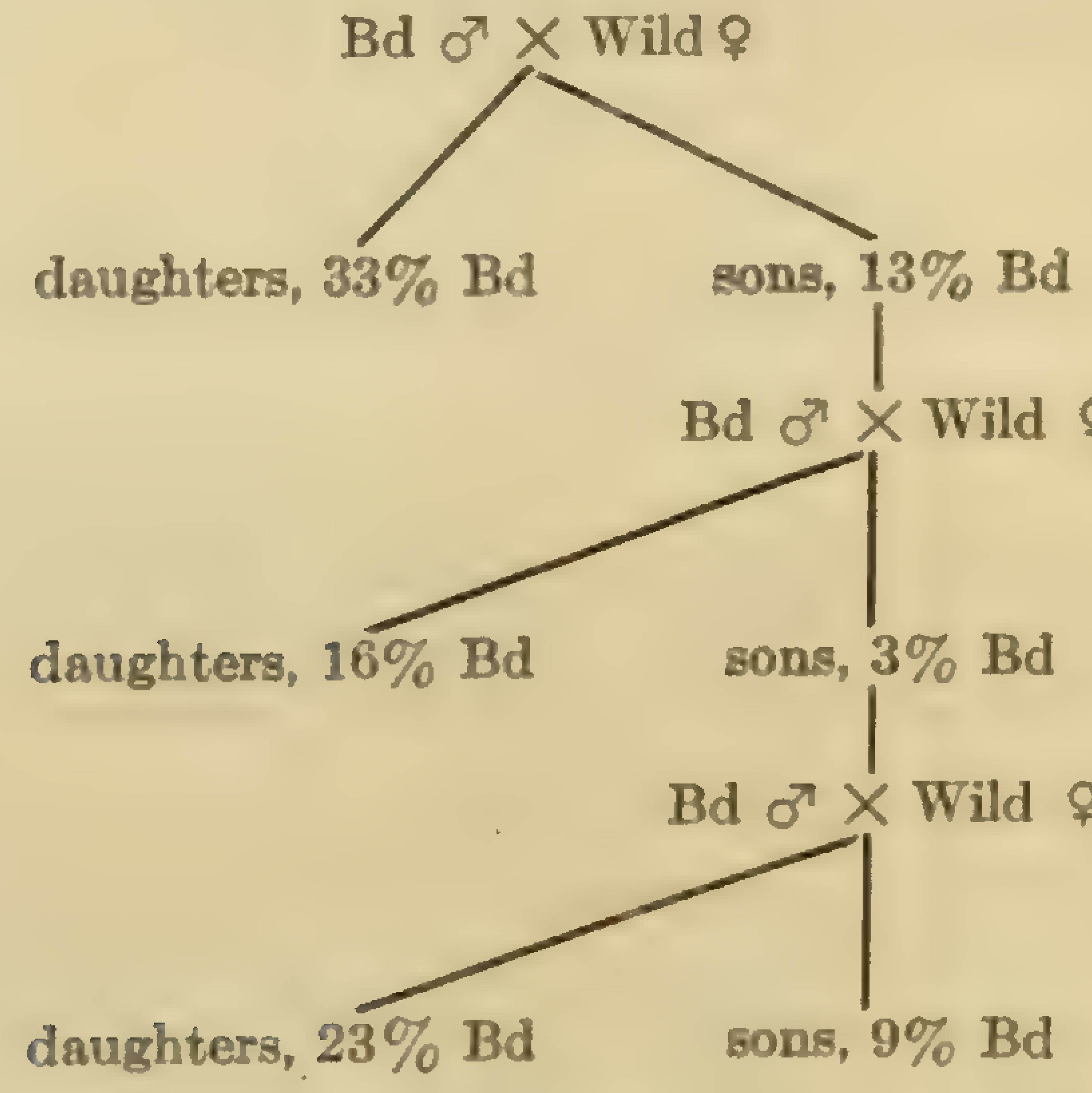
First Count	Last Count	First Count	Last Count	First Count	Last Count	First Count	Last Count	First Count	Last Count
36	7	10	0	10	33	10	13	3	7
4	0	42	24	1	0	25	24	51	30
10	0	71	25	8	1	24	0	23	11
20	0	0	1	19	7	11	3	15	12
1	0	5	5	3	0	32	0	43	8
48	20	64	15	36	10	40	0	42	0
45	4	37	3	25	3	46	9	32	6
37	40	17	6	18	0	60	0	50	40
33	15	10	0	47	10	16	0	29	4
21	0	10	0	28	20	52	0	56	29

Larger percentage of Beaded-winged offspring the first count, 44 broods.
Larger percentage of Beaded-winged offspring the last count, 5 broods.
Equal percentage of Beaded-winged offspring both counts, 1 brood.

the counts made in the first few days after the flies of any brood begin to hatch show almost invariably a very much larger percentage of Beaded-winged offspring than do the last counts made. This fact will be considered at some length in the section on environmental effects.

Enough has been said, at least, to show that, whether the results here described are genetic or environmental effects, the F_1 generation is remarkably inconstant with reference to the percentage of Beaded-winged offspring that appear. It is evident that this percentage can be readily altered by (1) changing the length of the period

CHART 2.



during which the brood is allowed to run; (2) by changing the parents from one bottle to another. Extensive studies of environmental effects have shown other ways in which the percentages can be altered, but of this we will treat later.

2. *Behavior in the Second Generation*

The question at once arises whether the Beaded and normal F_1 flies are alike genetically. To the solution of this problem two different breeding tests were applied: viz., matings of F_1 normal by normal, normal by Beaded, and Beaded by Beaded; and back crosses of both normal and Beaded to Wild stock. The results of these tests are given in Tables IV and V. These tables show that when

Beaded-winged flies of the F_1 generation are used as parents, more Beaded-winged young are produced than when normal-winged F_1 flies are used. This holds true for each

TABLE IV

MATINGS BETWEEN F_1 FLIES OF THE CROSS BEADED BY WILD, SHOWING PERCENTAGES OF BEADED OFFSPRING IN INDIVIDUAL BROODS

	Per Cent. of Flies Beaded													
	0–4.9	5–9.9	10–14.9	15–19.9	20–24.9	25–29.9	30–34.9	35–39.9	40–44.9	45–49.9	50–54.9	55–59.9	60–61.9	65–69.9
Normal × Normal	8	2	2	...	...	1	...	...	1	1	...	...	...	...
Normal × Beaded	1	...	...	...	...	1	...	3	1	...	2	...	...	...
Beaded × Beaded	...	...	...	...	...	...	...	...	...	1	2	1	1	1

TABLE V

BACK-CROSSES TO WILD OF F_1 FLIES OF THE CROSS BEADED × WILD, SHOWING PERCENTAGES OF BEADED OFFSPRING IN INDIVIDUAL BROODS

	Percentage of Offspring Beaded									
	0–4.9	5–9.9	10–14.9	15–19.9	20–24.9	25–29.9	30–34.9	35–39.9	40–44.9	45–50
Normal × Wild	9	....	....	....	....	....	....	....	....	....
Beaded × Wild	3	7	5	6	3	1	2	1	0	2

of the five crosses shown in the two tables. Normal-winged F_1 flies do, however, have some Beaded-winged offspring, both when mated among themselves, and also, though more rarely, when back crossed to Wild.

These F_2 and back-cross results give little satisfaction at first sight to the student of Mendelism. If we suppose that there is one gene on which the Beaded condition depends, and that it is partially dominant, then Beaded

TABLE VI

BEADED AND NORMAL OFFSPRING BY SEXES WHEN ONE PARENT IS BEADED AND THE OTHER WILD

	Beaded ♀♀	Normal ♀♀	Beaded ♂♂	Normal ♂♂	Per Cent. ♀♀ Bd.	Per Cent. ♂♂ Bd.
Father Beaded	1,246	4,488	948	4,481	21.7	17.5
Mother Beaded	894	2,959	1,139	2,684	23.2	29.8

and normal F_1 flies should give the same results when used as parents. Or if we were dealing here with a case like the "yellow mouse" case, in which homozygous yellows do not exist: that is, if homozygous "Beadeds" do not exist, then one quarter of the flies produced by two Beaded parents from the stock should be normal. But as was said before, the stock breeds true, every fly produced having Beaded wings.

It may be noted that a pair of F_1 normal flies usually produce less than 10 per cent. of Beaded offspring. If these normal flies carried a recessive gene for Beadedness, they should produce twenty-five per cent. Beaded offspring. The Beaded F_1 offspring, on the other hand, though they produced in all cases more than twenty-five per cent., did not produce 75 per cent. Beaded offspring, as they should have done if a single dominant gene for Beaded wings were heterozygous in them.

3. *Behavior in Third and Fourth Generations*

Beaded offspring, that appeared in the F_1 generation of the cross Beaded × Wild, were back crossed to Wild. The process was again repeated with the Beaded offspring that appeared, till four generations had been produced. The results of this test are given in Tables VII and VIII and in Chart 4.

A striking result is that an F_1 Beaded fly or even a fly of later generations heterozygous for Beaded wings some-

TABLE VII

REPEATED BACK-CROSSES OF BEADED-WINGED FLIES FROM THE CROSS BEADED BY WILD TO WILD STOCK TO SHOW PERCENTAGES OF BEADED-WINGED OFFSPRING. See Chart IV

	Family 1		Family 2		Family 3		Family 4		Family 5		Total	
	No. of Offspring	% Bd.	No. of Offspring	% Bd.	No. of Offspring	% Bd.	No. of Offspring	% Bd.	No. of Offspring	% Bd.	No. of Offspring	% Bd.
Generation 1	86	25.6	460	28.9	690	23.2	48	4.2	82	15.9	1,266	23.8
Generation 2	226	25.7	1,711	19.3	646	15.9	137	1.5	314	7.6	3,034	17.4
Generation 3	515	20.8	2,512	24.6	2,241	19.3	441	1.8	319	16.3	6,038	21.9
Generation 4	135	8.9	196	24.0	....	....	297	4.0	132	25.0	760	13.7

TABLE VIII

Normal Females from Family 2, Generation 2, Back-crossed to Wild Males, Showing Percentages of Beaded-winged Offspring

	Beaded	Normal	% Bd.
Type X	2	1,040	.02
Type Y	50	342	15.3

times has as large a percentage of Beaded-winged offspring when mated to Wild, as does a fly direct from pure Beaded stock when mated to Wild, though a comparison of Tables I and V shows that this is not the usual occurrence. This suggests at once the action of a lethal gene (Morgan, 1912*b*). Morgan has shown that in a certain stock of *Drosophila* there are twice as many females as males in the offspring of one half the females. No matter to what male such a female be mated, her daughters are twice as numerous as her sons, and one half of her daughters also repeat this phenomenon, and one half of the daughters of these again. This fact finds its explanation in the assumption that there is in one of the sex-chromosomes of such females a gene which prevents the development of any male which gets it.

Now if such a gene had the power of expressing itself as a dominant in those flies that carried it in the heterozygous condition, if, for example, it caused the wings to be Beaded, it would be possible to select such flies at sight, and these flies could then be depended upon to repeat the phenomenon. (Morgan accomplishes the same end by mating such flies to mutants carrying a gene with which the lethal gene shows close linkage, such as that for white-eyes. He then finds that the red-eyed females carry the lethal gene, unless, as rarely happens, a "cross-over" has occurred.)

Such a sex-linked lethal gene producing a dominant wing character has actually been found to occur in the case of a mutant which arose in the Beaded stock, and which will be discussed later. For the present we must note that if the lethal gene were not associated with sex, its presence could be detected by the absence of certain

expected ratios, or classes, or in some other peculiarity of genetic behavior. In the case before us, we found that the F_1 generation consisted of at least two types; viz., Beaded and not-Beaded flies. These were shown to differ genetically. To obtain such a result must mean that at least one of the parents was heterozygous in at least one gene. This result is however a fairly constant one; and by virtue of the long-continued inbreeding of the Beaded stock this heterozygosity must surely have been weeded out before now if there were no serious hindrance to homozygosity. The classic example of this sort of effect is that of the yellow mice.

But the development of Beaded wings can not be brought about by the action of a *single* lethal gene, for if this were true it would be impossible to obtain a stock of Beaded flies that would breed true, and yet such a stock, as has already been said, is the one from which these very crosses derive their Beaded ancestors. There must therefore be at least one pair of allelomorphs of which one member is effective in producing Beaded wings, and can exist in the homozygous condition and possibly also another pair of allelomorphs of which one member is a recessive lethal gene. We can explain many of the facts so far obtained on the supposition, that there are these two independently Mendelizing pairs of allelomorphs concerned in the production of Beaded wings. The pair containing the lethal gene we will call L (normal) and l (lethal); and the other pair B′ (Beaded) and b′ (normal). The occurrence of the two genes B′ and l in one individual usually causes such an individual to have Beaded wings, though Beaded-winged flies also occur which do not carry the lethal gene, but are homozygous for B′.

It should be possible then to isolate a stock of Beaded-winged flies not carrying this lethal factor, l. Such flies should give a much smaller percentage of Beaded-winged offspring in the F_1 generation of a cross with Wild stock (or perhaps none at all, if B′ were recessive), than would those flies carrying lL. Such a stock has not yet been ob-

tained, but occasionally a strain of Beaded flies is met with that gives only low percentages of Beaded-winged offspring. See, for instance, Family 4, Table VII. Possibly such a stock would not be recognized at once, especially if it were so affected by environmental conditions that even flies homozygous for the factor B′B′ sometimes had normal wings. Normal-winged flies, as will be pointed out in a later section of this paper, do very frequently appear in Beaded stock, but these flies when mated to each other appear to throw as many Beaded-winged offspring as do the Beaded-winged flies of the stock, and often 100 per cent. of their offspring have Beaded wings.

In this connection it will be of interest to recall that Chart 1, and Table I gave results that might be interpreted as evidence of the bimodal curve that should be expected if the above hypothesis is correct.

Normal females from the second generation of Family 2 were also back-crossed to Wild males. The results are given in Table VIII. Most of these normal females gave very few or no Beaded offspring (Type X) while two of them gave a considerable number of Beaded offspring (Type Y). The explanation here is perhaps that the type Y females were genetically like most of the Beaded females of an F_1 generation (on our hypothesis, B′ L b′ l) while the females of Type X were genetically lacking in the factors that are usually present in Beaded F_1 flies (*i. e.*, they were B′ L b′ L). That such an occurrence is not infrequent in *Drosophila* is seen in Table IV in which three broods out of fifteen raised from normal F_1 flies gave 25 per cent. or more of Beaded offspring though the other twelve broods gave less than fifteen per cent., and eight broods less than five per cent. of Beaded offspring. It seems certain therefore that there are two types of normal-winged offspring in the F_1 generation of the cross, Beaded by Wild; one of these is genetically like the Beaded flies of the same generation and the other is genetically different from its Beaded brothers and sisters.

Types X and Y have been found to occur in all of the

tests made of F_1 flies whether of matings to Wild stock or of matings to other mutants such as Black, Pink, Arc, Ebony, etc. Table XXVI shows these two types as they appeared in back crosses to normal Pink males of normal and Beaded females of the cross Pink Beaded by Wild. Here it was found that more of the normal than of the Beaded F_1 flies were of Type X, and conversely that more of the Beaded than of the normals were of Type Y.

It has not been possible to distinguish with certainty between these two types even by their offspring because of the large amount of fluctuation that occurs in the percentages of Beaded offspring. For example it would be difficult to say whether a fly giving five per cent. of its offspring Beaded would belong to Type X or Type Y.

It would be expected that Type Y would be given by those flies that carried both factors for Beaded, and Type X by those that lack the lethal factor, and it will be seen later that on the whole the evidence supports this view.

B. Crosses between Beaded Flies and Other Mutants

1. *The F_1 Generation*

If we examine the F_1 generation when Beaded flies are crossed to other mutants, *i. e.*, to flies of a stock that is perfectly normal so far as Beadedness is concerned, but which is unlike the normal Wild flies in some other wing character, or in eye color or body color, etc., we find an even greater amount of variability in the percentage of Beaded-winged offspring than in the F_1 generation of Beaded by Wild. (See Tables I and IX; also Charts 1 and 3.)

The details may be gathered from Table IX, where it can be seen that there is a certain specificity in the percentage of Beaded offspring that appear in any specific mating.

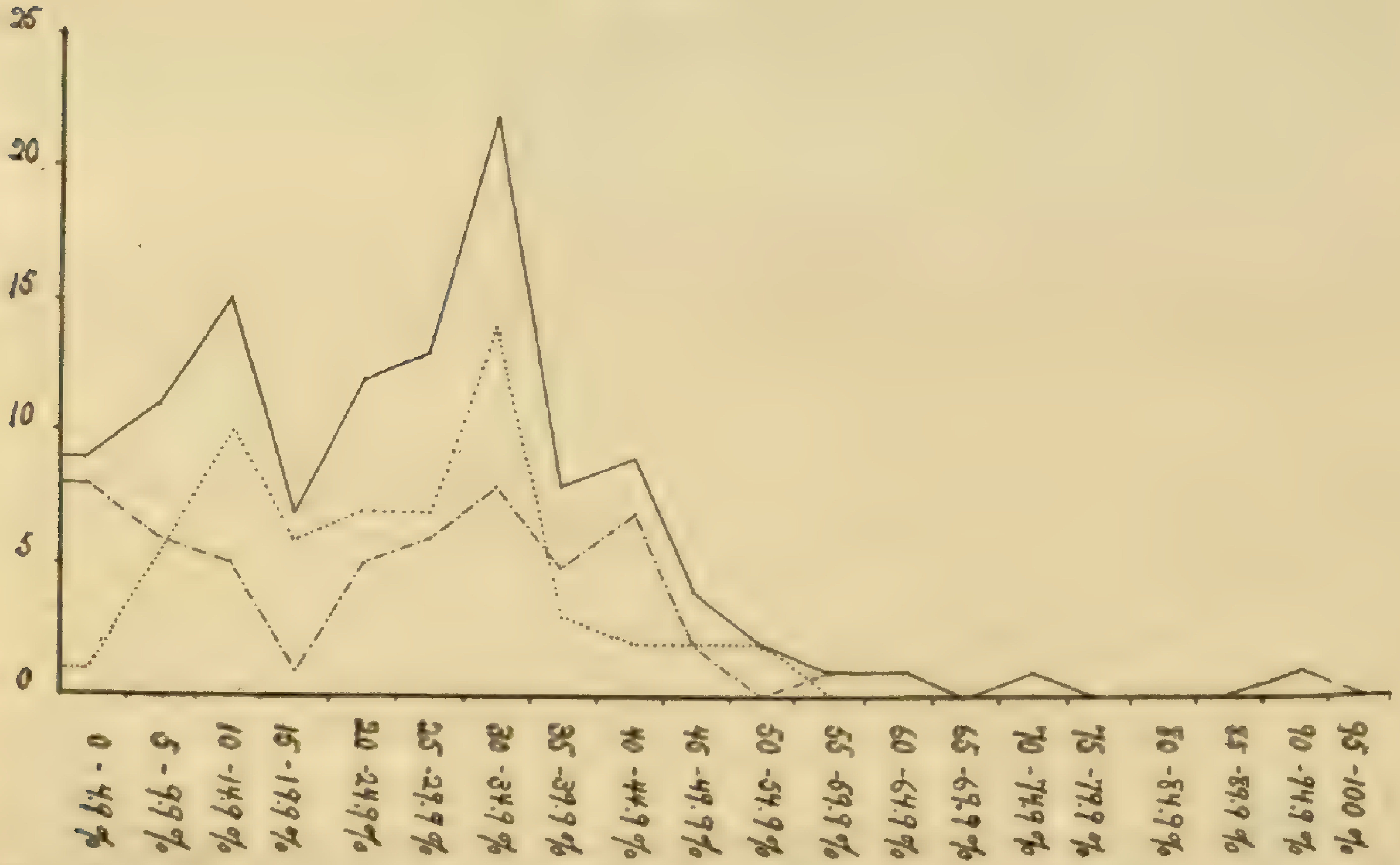
For instance, it appears that more of the offspring have Beaded wings if a cross is made with Vermilion-eyed flies than when Beadeds are mated to Pink-eyed

TABLE IX

THE PERCENTAGES OF BEADED-WINGED FLIES IN THE F_1 GENERATION OF CROSSES BETWEEN BEADED FLIES AND OTHER MUTANTS

Mutant Involved	Percentages																			
	0–4.9	5–9.9	10–14.9	15–19.9	20–24.9	25–29.9	30–34.9	35–39.9	40–44.9	45–49.9	50–54.9	55–59.9	60–64.9	65–69.9	70–74.9	75–79.9	80–84.9	85–89.9	90–94.9	95–100
Vermilion Yellow	..	1	..	..	..	1	1	..	..	1	..	..	..	..	..	..	..	..	..	..
Vermilion	..	..	..	..	1	..	..	1	4	..	..	..	..	..	..	..	..	..	..	..
Miniature Eosin	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..
White	..	..	..	..	..	1	4	3	1	1	..	..	..	..	..	..	..	..	..	..
Pink Beaded × White	2	..	1	..	..	2	..	..	1	..	..	..	..	..	..	..	..	..	..	..
Pink Beaded × Wild	4	4	4	1	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Pink	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Pink Ebony	..	..	..	..	1	1	..	..	1	..	..	..	1	..	..	..	..	..	..	..
Sepia	..	..	..	..	1	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..
Pink Black	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Black	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Purple Curved	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..
Truncate	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..
Vestigial	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..
Antlered	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..
Strap	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..
Total	8	6	5	1	5	6	8	5	7	2	..	1	1	..	1	..	..	..	1	..
Beaded × Wild (Table I)	1	5	10	6	7	7	14	3	2	2	2	..	..	..	..	..	..	..	..	..
Grand Total	9	11	15	7	12	13	22	8	9	4	2	1	1	..	1	..	..	..	1	..

CHART III



Distribution of broods giving certain percentages of Beaded-winged offspring in F_1 generation of Beaded × Normal (other Mutants or Wild). (See Table IX.)

flies, or more in the crosses with White-eyed flies than in those with Black body color. (In every case, where the contrary is not stated the flies are normal in other respects than the one named, *e. g.*, White-eyed flies in these crosses have Gray bodies and Long normal wings.)

No explanation of this specificity by the assumption of a segregation of factors in the germ cells appears to be available here, though such a possibility has not yet been ruled out, or can be ruled out till certain other phenomena are understood. The easiest way of "explaining" it is that the dominance of the genes for Beadedness varies in accordance with many other circumstances, among which are differences in the other genes present, such as those for Vermilion, White or Pink. Such an assumption as this, as will appear later, would seem to be fully in accord with the behavior of the genes for Beaded wings when in still different relationships.

It is assumed, then, for example, that the percentages of Beaded-winged flies in the F_1 generation of a cross between Beaded and White are higher than those in the F_1 generation of a cross between Beaded and Black, because the gene for Black is relatively to the gene for White eyes an inhibitor of Beadedness. It would appear as though a series might be made of the mutants of *Drosophila* beginning with those in which the genes for Beaded wings are most dominant and ending with those in which the Beaded genes are recessive. In order to construct such a series a large number of pairs would have to be made for each cross in order to determine the limits of variability of Beadedness for the cross concerned. The work would probably be greater than the value of the results obtained, and therefore the attempt has not been made to carry out this test. From what has been done incidentally in carrying out other experiments, it will be seen that in general the darker eye colors and body colors are associated with a low percentage of Beadedness in the F_1 generation, and the brighter colors with a higher percentage. This may, however, only be a coincidence.

2. *Linkage Relations*

(*a*) Sex Linkage

If in the crosses thus far described the sex of parents and offspring that show Beaded wings be considered, it may appear at first as though we may be dealing with a partially sex-linked gene. For it very frequently happens that when the mother is Beaded, and the father is normal (either of Wild stock or of some mutant stock not carrying Beadedness), more of the sons than of the daughters are Beaded. For example, in one such brood, there were 17 Beaded to 128 normal females, and 5 Beaded to 130 normal males, or 12 per cent. of the females and 3.5 per cent. of the males. Both of these examples were deliberately chosen because they were good examples of the phenomenon described. It would be possible to select from my records several examples of the reverse phenomenon, where Beaded females had more Beaded daughters than Beaded sons, and where Beaded males had more Beaded sons than Beaded daughters. Nevertheless, the records of all broods available have given the numbers shown in Table VI, where it appears that more sons are Beaded when only the mother is Beaded and more daughters when only the father is Beaded.

It may perhaps be significant, on the other hand, that when the mother is Beaded a *slightly larger percentage* of her daughters is Beaded than of the daughters of a Beaded male, while a *very much larger percentage* of her sons is Beaded than the sons of a Beaded male. In other words, it seems that the daughters are affected to approximately the same extent, whether they get their Beadedness from father or mother, while the sons are affected also by the mother, whether or not she carries Beadedness. This might mean that there is some gene in the sex chromosome that does not show except when other Beaded factors are present. That this is not the case will appear from Chart 2, which records three generations of flies in each of which the mother was normal (Wild)

and the father Beaded. This shows that although the father transmitted his Beadedness more to his daughters than to his sons, yet his Beaded sons also had the capacity to affect their daughters more than their sons, and these sons again repeated the phenomenon. Yet these males could not have received their X-chromosome from their father, unless non-disjunction (see Bridges, '13) had occurred. In fact, to produce the results here given non-disjunction must occur in one half the females of the Wild stock. Frequent tests with the Wild stock by practically all of the students in the laboratory make it certain that this is not the case. I also tested a considerable number of the females by mating them to sex-linked mutants and found no non-disjunction.

This apparent sex-linkage that does not follow the "ordinary rules" of sex-linkage must be left for the time being as one of the still unsolved problems. The only possibility of explanation that occurs to me is that the above-described effect would be produced if in the cytoplasm of the egg of the Beaded female something were present which is absent in the egg of the normal female, and to which the males are more responsive in their development than are the females. This suggestion has not a particle of cytological evidence to support it. Morgan (1912*d*) has suggested that the influence of cytoplasm may cause certain peculiar results obtained in crosses between Miniature-winged and Rudimentary-winged flies.

(*b*) Linkage to Sex-linked Genes

Matings of Beaded flies to flies with sex-linked characters, including Vermilion and Vermilion-yellow, have been made and the F_2 generation raised. No sign of linkage was observed. The F_2 figures are given in Tables X and XI. These cases definitely establish that there is no gene for Beaded wings in the X-chromosome.

Although no sex-linked gene for Beaded wings are known, there has arisen in the Beaded stock by mutation a fly with notched wings (Fig. 13) that proved to be

TABLE X

F_2 Counts from the Cross Vermilion ♀ × Beaded ♂

V.Bd. ♀	V.Bd. ♂	V.N. ♀	V.N. ♂	Red Bd. ♀	R.Bd. ♂	R.N. ♀	R.N. ♂
39	26	93	77	33	22	81	60

	% Bd.	Expected No. of Bd. if no coupling exists
Bd.V : N.V. = 65 : 170	27.6	65.4
Bd.Red : N.Red = 55 : 141	28.0	54.6
Bd.Total : N.Total = 120 : 311	27.8	(120)

TABLE XI

F_2 Counts from the Cross Vermillion Yellow × Beaded

Beaded Gray Red	Normal Gray Red	Beaded Gray Vermil.	Normal Gray Vermil.	Beaded Yellow Red	Normal Yellow Red	Beaded Yellow Vermil.	Normal Yellow Vermil.
165	227	35	34	41	34	50	88

	% Beaded	Expected No. of Bd. if no coupling exists
Bd.R. : N.R. = 206 : 261	44.1	201.7
Bd.V. : N.V. = 85 : 122	41.0	89.4
Bd.G. : N.G. = 200 : 261	43.4	199.1
Bd.Y. : N.Y. = 91 : 122	42.7	92.0
Bd.Total : N.Total = 291 : 383	43.2	(291.0)

13

caused by a dominant sex-linked factor lethal when homozygous. (See page 754.) It will be discussed under the name "Perfect Notched" and its peculiarities described in the section on "Mutation in Beaded Stock."

(c) Linkage to Second Chromosome Genes

For the reasons given, it seems certain that there is in the group of sex-linked genes no gene concerned in the production of Beaded wings. We shall later bring forward evidence to show that there is such a gene in the third chromosome group. (Sturtevant, 1913.) The crosses made with flies showing characters whose

genes are in the second chromosome are still perplexing; for while the second chromosome exerts an influence on the statistical results, as will be evident from the figures to be presented, the nature of this influence is not fully determined.

The second chromosome characters with which tests have been made are the wing characters, Arc, Curved, Vestigial, Antlered, and Strap,[1] the body color, Black; and the eye color, Purple.

Vestigial, Antlered, and Strap stand for wing characters of such a nature that it is not possible to distinguish Beaded-winged individuals if any of these other characters are also present. They are therefore of no use for determining whether or not there is a second chromosome gene for Beaded wings. The crosses between Beaded flies and flies with these characters do not especially interest us here. It may be said in passing, however, that in every case in the F_1 generation between these flies and Beaded flies, from 60 to 90 per cent. of the offspring had non-normal wings, and the author was put to serious straits to classify the new wing types that appeared. These were similar in all the crosses, however, and on the whole resembled Beaded wings.

In the F_2 generation, and in back crosses to Beaded Stock and to Vestigial Stock further complications arose with more new types of wings, including a new "mutation" which bred true from the start, and which will be discussed briefly and described under the name "Spread" in the section that concerns mutation.

We may now return to the crosses between Beaded flies and Black, or Purple, or Arc, or Curved. These crosses give results that can be used for the study of linkage, and they present in common a number of distinguishing

1 Strap Wings is a mutant much resembling Extreme Beaded in appearance but its mode of inheritance has not yet been worked out. It may be that it actually is Beaded plus some at present unknown gene. Beadedness is suspected to occur also in Vestigial and Antlered stock. This may very likely be true since Strap and Antlered arose in Vestigial, and Vestigial in Beaded.

characteristics. Tables XII to XX give the results in systematic form.

TABLE XII

F_2 Counts of the Cross Beaded ♀ × Curved ♂

	Beaded Curved	Normal Curved	Beaded Straight	Normal Straight	Exp. Bd. Curved	Exp. Bd. Straight
Type 1.........	4	61	16	246	4	16
Type 2.........	2	25	18	105	3.6	16.4

One of the most striking characteristics of these second chromosome crosses is that the F_1 flies fall into two classes or possibly into three classes with reference to the offspring that they produce. These classes I have called Type 1, Type 2, and Type 3.

In Type 1 there is no linkage between Beaded wings and the second chromosome character, but Beaded-winged flies occur with equal frequency in all classes of offspring. In Type 2 there is linkage of Beaded wings with the second chromosome characters, so that the Beaded wings appear more frequently in flies showing the characters of the Beaded parent. In Type 3, which occurs only a very few times and is not very marked except in Table XX, Beaded wings appear to a greater percentage in the offspring whose other characters are not those of the Beaded parent. (*I. e.*, "repulsion" occurs between the factor for Beadedness and that for the second chromosome character with which it entered the cross.) I do not wish to emphasize Type 3, but concerning the other two it is important to note that about one half of the F_1 flies seem to be of Type 1 and one half of Type 2.

TABLE XIII

F_2 Counts of the Cross Beaded ♀ × Arc ♂

	Beaded Arc	Normal Arc	Beaded Straight	Normal Straight	Exp. Bd. Arc	Exp. Bd. Straight
Type 1.........	39	200	184	970	38.+	185
Type 2.........	41	152	330	452	73	298

In Type 2 in the cases here adduced the linkage is

strongest with the character Arc and weakest with Black. If there is a gene in the second chromosome which aids in producing Beaded wings, it seems probable that it is located nearer to Arc than to Black and on the side of Arc away from Black.

TABLE XIV

BACK-CROSSES OF F_1 BEADED-WINGED MALES OF THE CROSS BEADED ♂ × PURPLE CURVED ♀ TO PURPLE CURVED FEMALES OF NORMAL STOCK

	Beaded Pr. Curved	Normal Pr. Curved	Beaded Red Straight	Normal Red Straight	Exp. Nor. Bd. Pr. Cv.	Exp. Nor. Bd. R. Strt.
Type 1.........	15	125	15	154	13.6	16.4
Type 2.........	2	29	28	27	10.8	19.2

It remains to consider Type 1, and to find the reason for the existence in the F_1 generation of flies whose offspring show no linkage between Beadedness and second chromosome characters, and in the same brood, flies whose offspring do show such linkage. The most obvious "explanation" would be, of course, that the factor in the

TABLE XV

BACK-CROSSES OF F_1 BEADED-WINGED FEMALES OF THE CROSS BEADED ♂ × PURPLE CURVED ♀ TO PURPLE CURVED MALES OF NORMAL STOCK

Brood 2 is of Type 3 for Purple and of Type 1 for Curved.

	Bd. Pr. Cv.	N. Pr. Cv.	B. Pr. St.	N. Pr. St.	Bd. Red Cv.	N. R. Cv.	Bd. R. St.	N. R. St.
Brood 1.............	7	49	1	22	1	17	16	61
Brood 2.............	10	47	4	6	0	12	14	71

second chromosome was a "lethal" such as the factor l, described in an earlier section of this paper. If this were the case, there should be some flies in the Beaded stock homozygous for L, the normal allelomorph of this gene, and also for B′, *i. e.*, B′LB′L. These flies should have fewer Beaded offspring than those heterozygous for l, and none of these F_1 offspring should give linkage with second chromosome characters. As a matter of fact, in the F_2 results given in Table XVI for Beaded by Black, no linkage was observed; but this case is not good evidence, for it was made in the first attempts to solve the problem of Beaded wings, and I had not yet learned the

value of F_1 counts, matings in pairs, and back-crosses to normal. It stands however as the only evidence of its sort that I can give at present.

TABLE XVI

F_2 COUNTS OF THE CROSS BEADED ♀ × BLACK ♂

	Beaded Black	Normal Black	Beaded Gray	Normal Gray	Expected No. Bd. Bl.	Expected No. Bd. Gray
Type 1.........	19	375	82	1602	19	82

Type 3 is not easy to explain. There are no known cases of this sort elsewhere in *Drosophila* and I prefer not to attempt to answer this question at present.

TABLE XVII

BACK-CROSSES OF F_1 MALES OF THE CROSS BEADED ♂ × BLACK ♀ TO BLACK FEMALES OF NORMAL STOCK

	Beaded Black	Normal Black	Beaded Gray	Normal Gray	Expected No. Bd. Bl.	Expected No. Bd. Gray
Type 1.........	7	162	9	187	7.3	8.6
Type 2.........	5	110	40	97	20.5	24.5

In general, it may be noted that technical difficulties have disturbed the crosses with second chromosome characters. The wing character Arc is not always easy to recognize, as it is very often nearly normal in appearance. On the other hand, the flies with Curved wings, though always distinct, occasionally get "stuck up" with the food and in their bedraggled condition it can not always be determined whether or not the wings are Beaded as well as Curved. I was at first inclined to attribute the apparent coupling (which was discovered for Arc and for Curved before it was discovered for Black) to errors made in the counts.

As for Black, the F_1 and later generations give a much lower percentage of Beaded offspring than do most other crosses, and this necessitates raising large numbers of offspring. The results are, however, trustworthy when obtained.

The crosses with Purple-eyed flies presented no difficulties but ran smoothly aside from the fact that the purple-eyed flies had Curved wings, and as remarked above, Curved wings sometimes get bedraggled.

TABLE XVIII

BACK-CROSSES OF F_1 FEMALES OF THE CROSS BEADED ♂ × BLACK ♀ TO BLACK MALES OF NORMAL STOCK

	Beaded Black	Normal Black	Beaded Gray	Normal Gray	Expected No. Bd. Bl.	Expected No. Bd. Gray
Type 1.........	5	78	2	91	3.3	3.7
Type 2.........	5	457	28	493	15.5	17.5

(*d*) Linkage to Third Chromosome Genes

We have said tentatively that there was perhaps a non-sex-linked lethal gene for Beaded wings in the second chromosome, and that possibly the cytoplasm carried by the egg disposes males toward or away from Beadedness according to whether the fly that bore the egg was or was not Beaded. These relations are not securely determined, and the data are still incomplete. The relation of Beaded wings to characters whose genes are in the third chromosome is much clearer. All crosses that bear on this problem point to one fact, namely, that there is a gene for the production of Beaded wings in the third chromosome, and that this gene is very closely linked to Ebony, and very loosely linked to Pink. Tests have been made between Beaded and the third chromosome characters, Maroon, Sepia, and Pink eyes and Ebony body color.

TABLE XIX

F_2 COUNTS OF THE CROSS PINK BEADED ♂ × BLACK ♀

	Pink Bd. Bl.	Pink N. Bl.	Pink Bd. Gray	Pink N. Gray	Red Bd. Black	Red N. Black	Red Bd. Gray	Red N. Gray
Type 1 (?)	2	25	20	57	0	45	3	278

	Expected No. Bd. if no coupling occurs
Bd.Pink : N.Pink = 22 : 82....................	6
Bd.Red : N.Red = 3 : 323	19
Bd.Black : N.Black = 2 : 70....................	4
Bd.Gray : N.Gray = 23 : 335....................	21
Bd.Total : N.Total = 25 : 405	(25)

In the cross of Beaded by Maroon-eyed flies, 1,369 flies were raised in the F_2 generation. Fifty-seven of these flies had Beaded wings; only one of the Beaded-winged flies had Maroon eyes, while fifty-six were red-eyed. (See Table XXI.)

TABLE XX.

Back-crosses of F_1 Females of the Cross Pink Beaded ♂ × Black ♀ to Pink Black Males from Normal Stock

	Pink Bd. Black	Pink N. Black	Pink Bd. Gray	Pink N. Gray	Red Bd. Black	Red N. Black	Red Bd. Gray	Red N. Gray
Type 1.....	5	98	8	113	5	92	1	122
Type 3.....	12	68	6	58	7	78	3	76
Totals ...	17	166	14	171	12	170	4	198

	Expected No. Beaded if no coupling occurs
Bd.Pink : N.Pink = 31 : 337..................	23
Bd.Red : N.Red = 16 : 368....................	24
Bd.Black : N.Black = 29 : 336................	23
Bd.Gray : N.Gray = 18 : 369..................	24
Bd.Total : N.Total = 47 : 705................	(47)

F_1 males of the cross Sepia by Beaded were back-crossed to normal Sepia females. Inasmuch as cross-overs probably do not occur in the male (Morgan, 1912*c*), no Beaded Sepia flies should occur in the offspring of this cross. Table XXII shows that none occurred. The numbers are not large, but since they are entirely in accord with the other third chromosome results, it was not thought worth while to increase them. That apparent cross-overs may very rarely occur will appear possible when we consider the results of crossing Beaded by Pink, and the probable significance of the phenomenon will be considered.

TABLE XXI

F_2 Results of the Cross Beaded ♀ × Maroon ♂

Bd. Maroon	N. Maroon	Bd. Red	N. Red	Exp. Bd. N.	Exp. Bd. R.
1	318	56	994	13	44

In F_2 counts of the crosses involving Beaded and the body color Ebony, totaling 4,417, in which 1,205 Beaded-winged offspring occurred, not one had the body color Ebony, and only eleven had Pink eyes. Repeated attempts

to obtain Ebony flies with Beaded wings have failed. The possibility that for some "inherent peculiarity" an Ebony fly can not have Beaded wings has suggested itself,

TABLE XXII

BACK-CROSSES OF F_1 BEADED MALES OF THE CROSS BEADED ♂ × SEPIA ♀ TO SEPIA FEMALES OF NORMAL STOCK

Bd. Sepia	N. Sepia	Bd. Red	N. Red
0	134	9	132

and although this would seem very improbable, it may nevertheless be the fact. At any rate, it appears that Beadedness either depends on genes which in the presence of the Ebony body color are completely recessive, or that the third chromosome gene for Beadedness, B′, lies so close to that for Ebony that cross-overs are extremely rare even in the female.

TABLE XXIII

F_2 RESULTS OF THE CROSS BEADED ♀ × EBONY ♂

Beaded Ebony	Normal Ebony	Beaded Gray	Normal Gray
0	151	17	525

Very extensive experiments were carried out with Pink-eyed flies. The important facts brought out are presented in condensed form in Tables XIX, XX, and XXIV–XXIX.

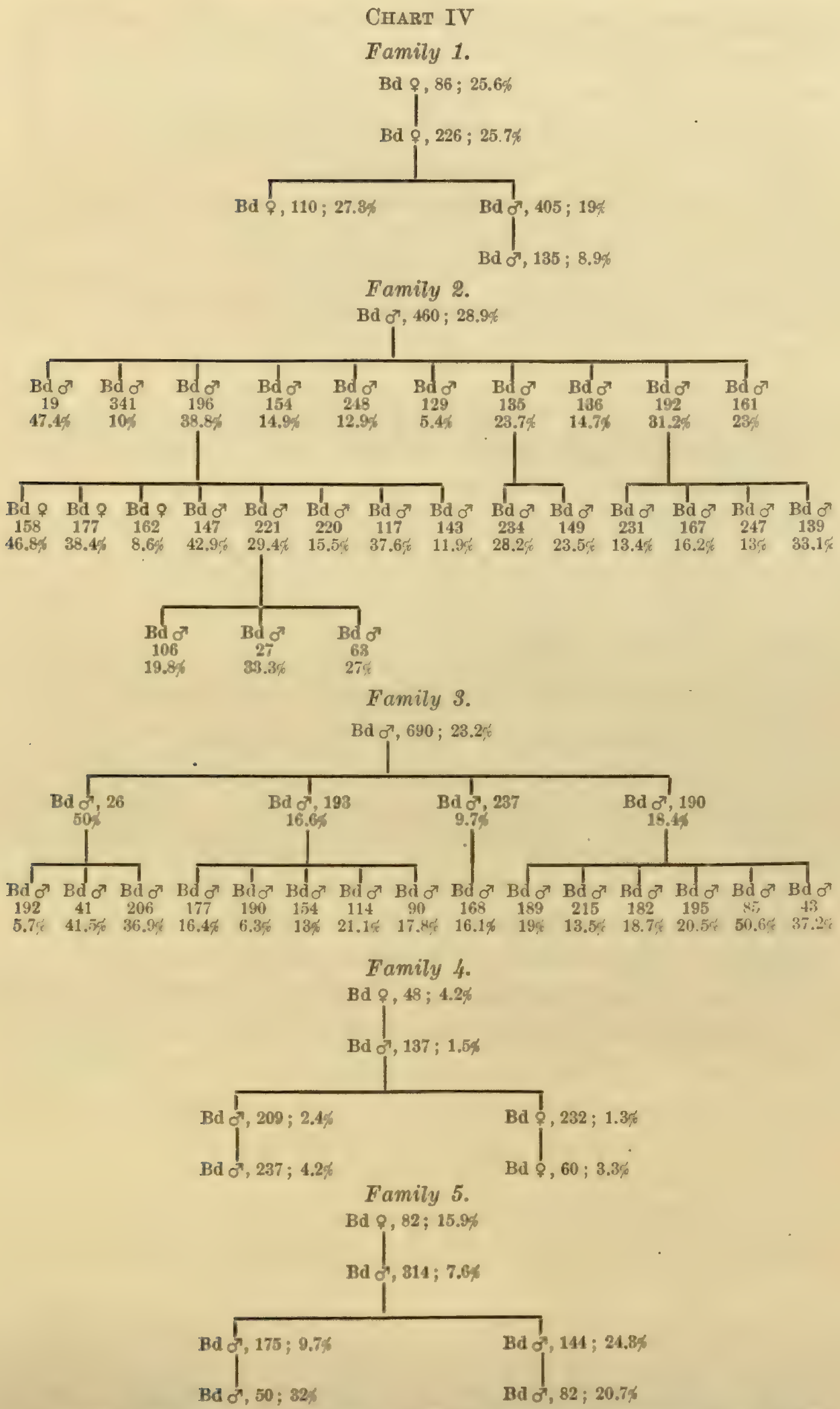
In Table XXIV are shown the F_2 counts for Beaded by Pink Ebony. From the eleven Pink Beaded flies obtained a new stock was derived, which was "purified" by a few

TABLE XXIV

F_2 RESULTS OF THE CROSS BEADED ♀ × PINK EBONY ♂

Bd. P. Eb.	N. P. Eb.	Bd. R. Eb.	N. R. Eb.	Bd. P. Gray	N. P. Gray	Bd. R. Gray	N. R. Gray
0	847	0	182	11	157	1,177	1,350

	Expected No. Bd. if no coupling occurs
Bd.Ebony : N.Ebony = 0 : 1029	328
Bd.Gray : N.Gray = 1188 : 1507	860
Bd.Pink : N.Pink = 11 : 1004	324
Bd.Red : N.Red = 1177 : 1532	864



Repeated back-crosses of Beaded × Wild in successive generations, showing sex of Beaded parent, number of offspring, and percentage of offspring with Beaded wings.

generations of selection, and now gives approximately 100 per cent. Beaded offspring, though no selection has been practised for nearly a year. This stock has been used in one series of crosses to supplement another series in which Pink and Beaded enter the cross from opposite parents. The results in each case are essentially similar, and show that when Beadedness enters with Red it comes

TABLE XXV

F_2 Results of the Cross Pink Beaded × Wild

Bd. Pink	Normal Pink	Beaded Red	Normal Red	Exp. No. Bd. P.	Exp. No. Bd. R.
171	213	366	964	120	417

out more with Red than with Pink. They show that in the F_1 female crossing over occurs almost independently of Pink, so that almost the same percentage of Beaded-winged individuals appears in each class, though usually the class that is similar to the Beaded parent is considerably the largest. In Table XXVII, however, a record is given in which a very considerable "repulsion" occurred, and the high Beaded class is not Pink Beaded, as is there expected, but Red Beaded. The results from back-crosses of the brothers of these females to Pink normal stock show that no mistake was made in recording the cross, which therefore, though somewhat surprising, must stand.

TABLE XXVI

Back-crosses of F_1 Females of the Cross Pink Beaded × Wild to Pink Males of Normal Stock

	Bd. Pink	N. Pink	Bd. Red	N. Red	Exp. No. Bd. P.	Exp. No. Bd. R.
Type X........	3	333	2	337	2.5	2.5
Type Y........	71	332	58	369	62.6	66.4
Total........	74	665	60	706	65	69

The tables show also that in the males, crossing over is of very rare occurrence, if, indeed, it occurs at all. The records show that out of 566 Beaded flies (Tables XXVII and XXIX) which occurred as the offspring of an F_1 male

back-crossed to Pink normal stock, six flies of the cross-over class appear. For reasons to be mentioned, it is improbable that these represent cross-overs, however, but rather they may be due perhaps either to the presence of the second chromosome gene, l, which usually does not manifest itself in the absence of the third chromosome gene, or to mutation, or to some unknown abnormality. Through carelessness only one of these males was tested

TABLE XXVII

BACK-CROSSES OF F_1 MALES OF THE CROSS PINK BEADED × WILD TO PINK FEMALES OF NORMAL STOCK

Bd. Pink	N. Pink	Bd. Red	N. Red	Exp. No. Bd. P.	Exp. No. Bd. R.
56	710	5	805	29	32

or used further in breeding. They were very slightly Beaded, and had only a very slight "nick" at the tip of the wing, even smaller than that shown in Fig. 3. The single Pink Beaded male mentioned in Table XXIX was mated to several females but was sterile. Another test is also possible, and was made as follows. Pink normal males and females from Table XXIX, which of course should not carry the third chromosome gene for Beaded

TABLE XXVIII

REPEATED BACK-CROSSES OF F_1 FLIES OF THE CROSS PINK BEADED × WILD TO PINK FLIES OF NORMAL STOCK

	Bd. Pink	N. Pink	Bd. Red	N. Red	Exp. No. Bd. P.	Exp. No. Bd. R.
F_1 ♀ ×Pink ♂. Type X	1	228	1	272	1	1
F_1 ♀ ×Pink ♂. Type Y	24	379	79	383	48	55
Total	25	607	80	655	49	56
F_1 ♂ ×P ♀	7	133	0	135	3.5	3.5

wings, were then mated together, and among their 374 offspring three males with slight "nicks" at the tip of their wings, exactly like those of the Pink Beaded male before mentioned, were produced. One of these males was sterile. One of the remaining two was fertile, but

gave no Beaded offspring either in the first generation or in the F_2 generation, although nearly one thousand of his grandchildren were carefully examined. The remaining male was abundantly fertile and had one son exactly like his father in appearance (with a slight nick at the tip of the wings). The rest of his offspring were normal. This son was sterile.

TABLE XXIX

BACK-CROSSES OF F_1 FLIES OF THE CROSS BEADED × PINK TO PINK FLIES OF NORMAL STOCK

	Beaded Pink	Normal Pink	Beaded Red	Normal Red	Exp. Bd. Pink	Exp. No. Beaded R.
F_1♂ ×Pink ♀ ..	1	859	504	580	223	282
F_1♀ ×Pink ♂ ..	70	114	114	106	84	100

The results of these tests with five of these supposed "cross-over" males show clearly that they were not normal Beaded flies. As said, they might represent mutations, or the dominance of the gene l, or some abnormality. These are mere guesses, but since there are no authentic cases on record in *Drosophila* of crossing over in the male sex in those cases where the mutants dealt with are well known genetically, *i. e.*, since the only apparent cases occur in the Beaded wings and some of the other not well-known and peculiar mutants of *Drosophila,* we are not justified in assuming that such crossing over takes place here.

III. THE EFFECT OF ENVIRONMENTAL CONDITIONS UPON THE PRODUCTION OF BEADED WINGS

A. General Statement

If we have so far interpreted the evidence correctly we may formulate the following statement as a provisional hypothesis. A gene B′ located in the third chromosome near that for Ebony is directly responsible for the production of Beaded wings. By itself in the homozygous condition, the fly bearing it may have normal wings, though it usually will have wings somewhat Beaded. In the heterozygous condition, it is rarely, though sometimes,

dominant. The conditions so far presented which cause it to be dominant are two. (1) The presence of a gene l in the second chromosome which can not exist in the homozygous condition. (2) The influence, particularly noticeable in the males, of non-chromosomal constituents of the egg from which the individual arose, so that if the mother had been Beaded, the appearance of Beaded wings in her sons would be increased, and if the mother had been normal the appearance of Beaded wings in her sons would be reduced.

Certain facts already brought out (namely, those presented in Tables II and III) show that the tale is not yet told. Our hypothesis does not explain the fact that from definite numbers of eggs laid at different periods in the life of an individual very different percentages of Beaded-winged offspring arise, and these differences do not form a definite series progressing to or from a high percentage as the individual grows older, but are extremely irregular. We have not gained control over this phenomenon, but the evidence we have to present points strongly to the suggestion that the environmental conditions are the final determiners of the percentage of the Beaded-winged offspring. This environmental control might lie in three distinct methods: (1) The destruction of a certain class of offspring by their differential viability. (2) In the case of Table III the results might be explained on the theory that Beaded flies had a shorter life cycle. This supposition has, however, been disproved as follows. Five non-virgin females from Beaded-winged stock and five non-virgin females from normal-winged stock were put together without males in the same bottle. When the offspring began to hatch they were examined daily. During the first three days 73 flies hatched, of which 11, or 15 per cent., had Beaded wings. During the following five days 261 flies hatched, of which 54, or 20 per cent., had Beaded wings. Since I was particular to take Beaded flies several days old as the parents of these Beaded offspring, the experiment shows that if there is any difference in the length of the larval life, that of normal-winged flies is

the shorter. (3) The determination of whether or not a fly of a given germinal constitution shall have Beaded wings. The first of these effects is probably not the significant one, in view of the following facts.

Although as a rule F_1 normal flies give few Beaded offspring, and F_1 Beaded-winged flies relatively many, nevertheless, as has been said, at times normal flies give a high percentage of Beaded offspring and, occasionally, Beaded flies give a low percentage. This can only mean that the dominance of the factor B′ is variable, and considering the large number of times that it shows itself as a recessive, it must be that this varying dominance has a marked effect on the percentage of Beaded-winged offspring that appear.

The possible amount of variation in the environment surrounding a brood of *Drosophila* developing under laboratory conditions is enormous, even when the attempt is made to keep conditions constant. These variations depend upon the exact ripeness of the bananas used as food, the length of time the food has been fermenting, the amount of food and filter paper used, the size of the bottle in which the larvæ are developing, the tightness of the cotton plug, the temperature of the laboratory, etc. Due to these causes there arise very great differences in the relative moisture content and carbon dioxide content. If the food is not properly prepared it may rot instead of fermenting, or it may mould, or the reaction may be in one bottle quite alkaline and in another very acid. A perfect control thus becomes an impossibility, and therefore the experiments to be described must be considered as trials only, and not as decisive tests.

In all the experiments on this subject, Beaded flies of pure stock were mated to normal flies of Wild stock in order to learn the effect of particular environments on the percentage of Beaded offspring in the F_1 generation. On our hypothesis, the pure Beaded flies from stock should be of two kinds, viz., those with the lethal gene l (*i. e.*, B′lB′L), and those without l (*i. e.*, B′LB′L). Correspondingly there should be two types of offspring in the F_1

generation, one of which (B′lb′L) should have a considerably higher percentage of Beaded offspring than the other (B′Lb′L). If it is possible, however, that B′ should be dominant in the heterozygous condition and in the absence of l, then it should also be possible theoretically to produce an F_1 generation every individual of which should have Beaded wings, while those with l as well as B′ (constituting one half the progeny) should have a more extreme form of Beading. In practice it is not usual even under the best of conditions to get more than 40 per cent. of Beaded-winged flies, while, as has been seen, the average amount is about 25 per cent.

B. The Effect of Relative Moisture

Table XXX and Charts 5 and 6 present the data for

TABLE XXX

Percentages of Beaded-winged Flies in the F_1 Generation in Relatively Wet and Dry Bottles. Not Done in Pairs, but Each Bottle Contained Several Pairs

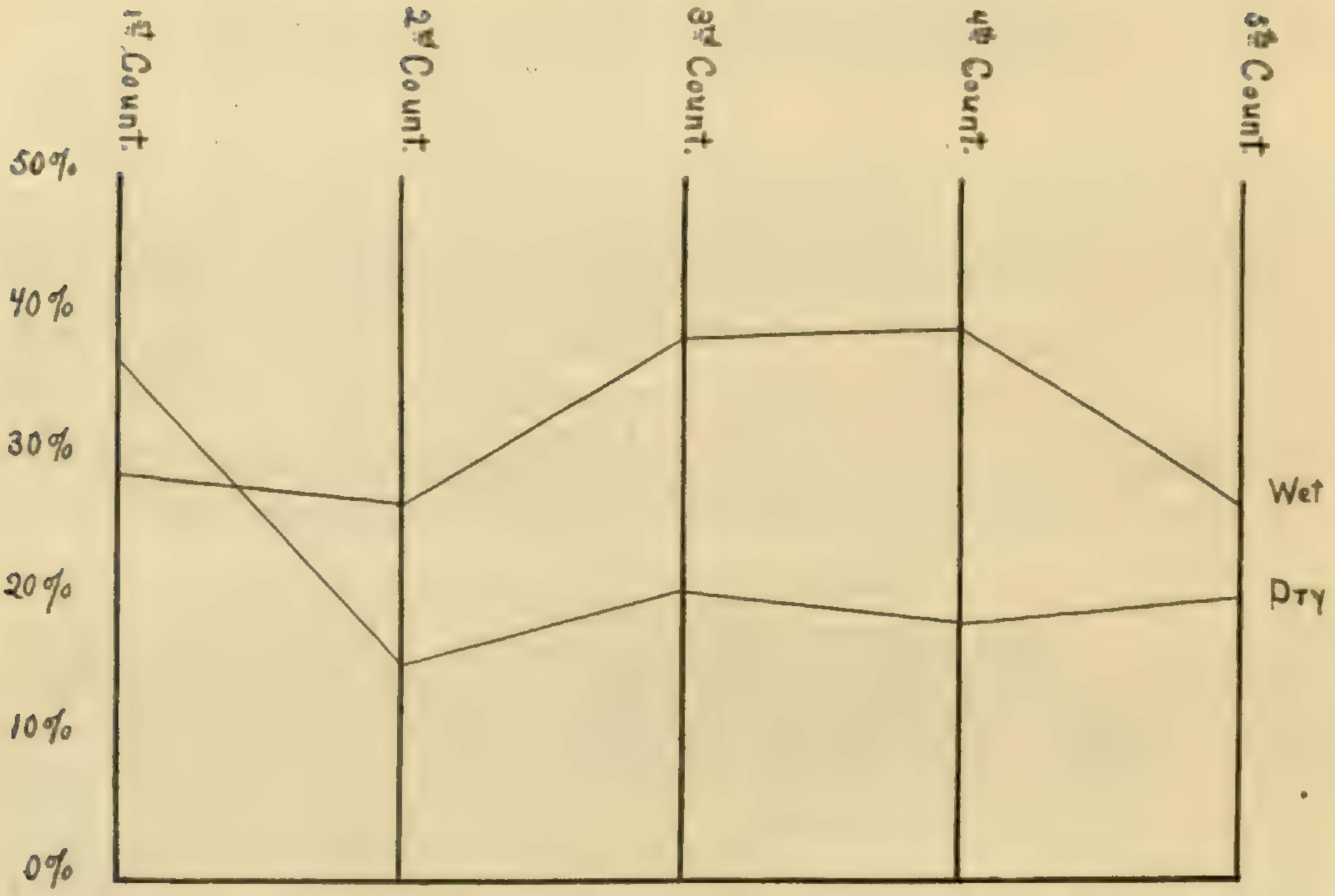
	Dry Bottles				Wet Bottles					
	No. 1		No. 2		No. 3		No. 4		No. 5	
	No. Flies	% Bd.	No. Flies	% Bd.	No. Flies	% Bd.	No. Flies	% Bd.	No. Flies	% Bd.
1st count	38	31.6	32	43.7	26	26.9	14	28.6	26	30.8
2d count	122	14.7	58	17.2	79	32.9	87	20.7	131	26.7
3d count	34	20.6	19	21.1	24	41.6	16	37.5	37	37.9
4th count	33	27.3	34	8.8	39	35.9	17	41.2	43	41.7
5th count	59	20.3	72	25.0	35	31.4	30	36.7	53	18.9
6th count	95	10.5	37	35.1						
Total	281	17.8	252	24.6	203	33.5	164	28	290	29.3
Total Dry 533	% Bd. 20.5				Total Wet, 657			% Bd. 30.3		

Counts not made every day.

Bottle No. 2 was very dry and the flies very small during time of last two counts.

this test. The parents were put into bottles of similar size with plenty of food. In three of these bottles the food was very wet and from time to time juice was added in sufficient amount to keep the food saturated. The other two bottles were made relatively dry by putting a

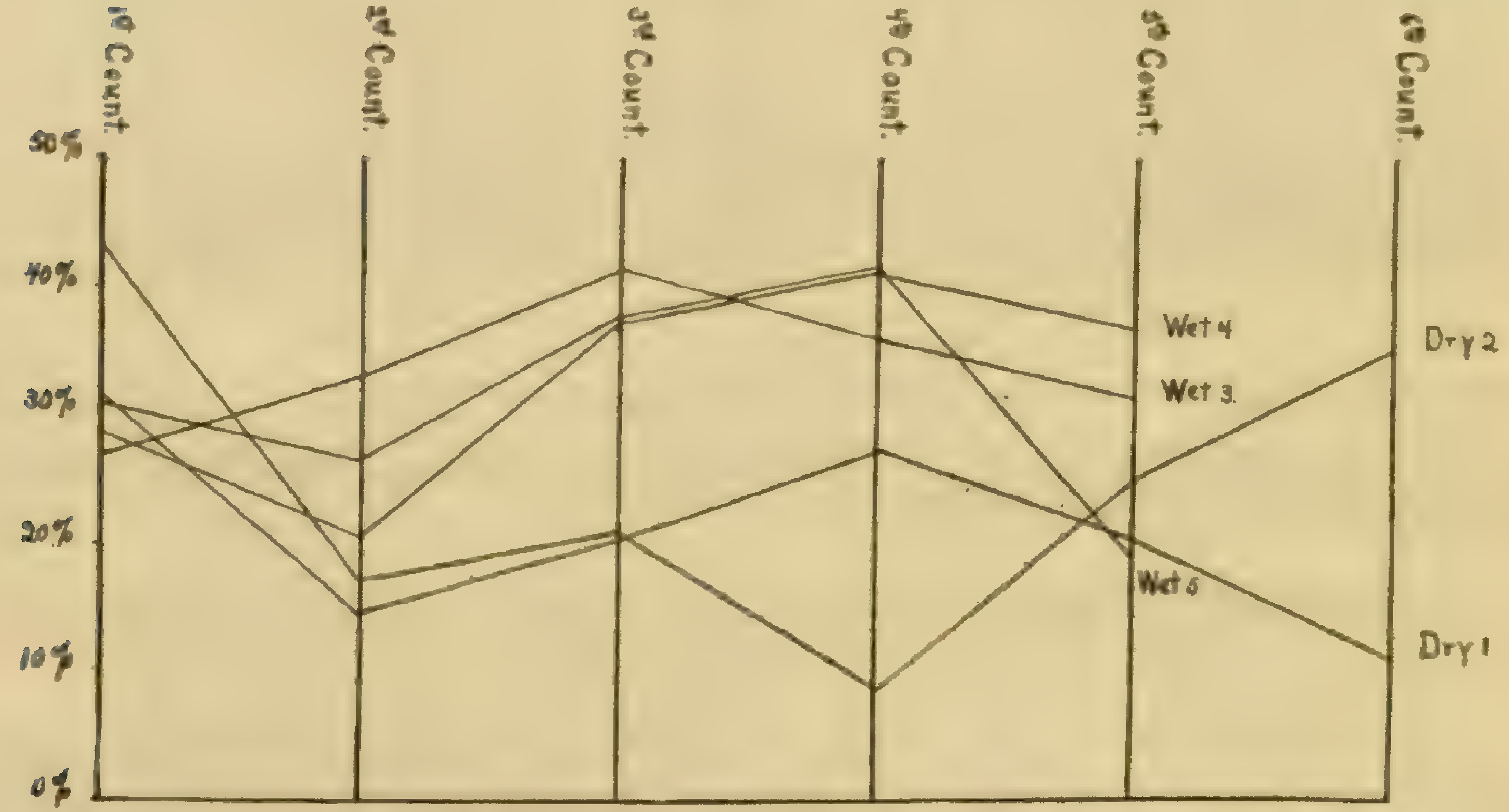
CHART V



Effect of Relative Moisture in Food on Percentages of Beaded-winged Flies in F_1 Generation of Beaded × Wild.

large amount of filter paper into the bottle at night and removing it the following morning. After two or three days of this treatment the bottles were so dry that I did not venture to carry the process farther; the flies from

CHART VI



Effect of Relative Moisture in Food on Production of Beaded Wings, as shown by Individual Bottles.

these dry bottles were rather small and in bottle No. 2, they were extremely small in the last two counts.

From Chart 6, where the records are given of the individual bottles, it will be seen that there is a good deal of irregularity from day to day.

Special attention should be called to the curve of production of bottle 2, which beginning with a high percentage of Beaded offspring gives fewer and fewer for the first four counts (about six days) and then the percentage rapidly mounts again. The offspring given during the last two counts were of surprising minuteness and gave as high a percentage of Beaded individuals as the average of all the bottles on the first day. It has been suggested that it may not be wetness or dryness or any one specific thing that brings out the Beadedness, but conditions that are unfavorable to the organism as a whole, resulting in poor nourishment. It has frequently been

TABLE XXXI

THE INFLUENCE OF ACID, ALKALINE, AND FRESH FOOD ON THE DEVELOPMENT OF BEADED WINGS

	Bd. ♀	Bd. ♂	N. ♀	N. ♂	Per Cent. Bd. ♀	Per Cent. Bd. ♂	Per Cent. Bd. Total
Food Sour							
Mother Beaded; Father normal	26	40	151	129	14.7	23.8	19.1
Father Beaded; Mother normal	9	7	60	61	13.0	10.3	11.7
Food Fresh							
Mother Beaded; Father normal	23	25	85	92	21.3	21.4	21.3
Father Beaded; Mother normal	54	15	147	164	26.9	8.4	18.2
Food Alkaline							
Mother Beaded; Father normal	36	41	40	41	46.8	50.0	48.7
Father Beaded; Mother normal	28	16	57	58	32.9	21.6	27.7

noted that those bottles which gave very tiny flies gave also a higher percentage of Beaded individuals than the bottles whose flies were of average size. On the other hand, the first flies of a brood are almost invariably larger than the later ones, and yet, as has been seen, they are more Beaded. This is a paradox, but the behavior of bottle No. 2 suggests that as a hatch proceeds and the bottle becomes drier, there may be a certain optimum point for the production of normal winged offspring, and

that this point is so low that the flies are poorly nourished for lack of water, though they can survive an even greater water reduction.

It is, perhaps, needless to say that an effort has been made after these experiments to keep the moisture content high and fairly uniform in cases where other environments were being tested.

C. The Effects of Covering with Paraffine the Mouth of the Bottle in which the Flies are Developing

On observing that the proportion of Beaded to Normal offspring was lowered as a hatch continued, it seemed possible that this might be due to one or to both of two causes: (1) The diminishing water content. This matter has already been considered. (2) To a changing carbon-dioxide content. When a brood is first counted the cotton plug that has been for several days in the mouth of the bottle is removed, and in removing the flies the air within the bottle is very apt to be much changed. With this possibility in mind a number of bottles were supplied with food and flies, and after ten days (when the larvæ were beginning to pupate) the parent flies were removed, a little new food put into the bottle and a paraffine cap melted over the cotton so that the bottles were tightly

TABLE XXXII

Counts of Seven Broods which Hatched During Two Periods, the First of Which was Spent in a Bottle Sealed with Paraffine, and the Second in a Bottle Covered with Cheese Cloth. Bottle No. 7 was not Sealed with Paraffine but had been Lightly Stoppered with Cotton

	Bottle 1		Bottle 2		Bottle 3		Bottle 4		Bottle 5		Bottle 6		Bottle 7	
	No. Flies	% Bd.	No. Flies	% Bd.	No. Flies	% Bd.	No. Flies	% Bd.	No. Flies	% Bd.	No. Flies	% Bd.	No. Flies	% Bd.
1st count	75	36	82	40	54	44	51	45	59	29	18	39	87	28
2d count	54	9	32	3	17	6	22	18	36	0	15	13	52	2

Total, first count, 426, per cent. Bd., 36.
Total, second count, 228, per cent. Bd., 6.
Total, both counts, 654, per cent. Bd., 25.

sealed. At the same time other bottles were very loosely covered with a light cotton plug. The bottles remained covered till flies had been hatching for four or five days and then the plugs were removed and the flies counted. The paraffine plugs were not replaced; after carefully renewing the air in the bottles, they were covered with cheese cloth and their brood counted again in four days. The results of this test are given in Table XXXII. The results are striking enough at first sight, but I do not know just what their significance is. They show exactly the same phenomenon that is described earlier and illustrated in Table III. They are more striking than any case I have yet found of the sort, and yet the first inference drawn, viz., that the markedly higher percentage of Beaded flies in the first count is due to these flies having undergone their late development in a "close" atmosphere, must be qualified by the statement that "close" does not refer to the carbon-dioxide content.

At first suspecting this to be the case, I made an apparatus by means of which fresh air could be drawn through a bottle during the entire development of the brood. By this means the carbon-dioxide content could not become very high. In order to prevent drying out, a large amount of food was put into the bottle and the air which was to enter the bottle was first passed through water. The hatching period was prolonged in the cool sink. The results were decisive. One hundred and sixty-nine flies were hatched in the first four days, of which 32 per cent. were Beaded. One hundred and eighty-four flies were hatched in the next four days, of which 10 per cent. were Beaded.

The same flies that were the parents of this brood were in the meanwhile transferred to another bottle, which was covered with paraffine. The first four days of hatching gave 108 flies, of which 15 per cent. were Beaded.

This case shows conclusively that the carbon-dioxide content of the bottles is not the feature of the closed bottles that determines whether or not a fly shall have Beaded wings. It leaves the question still unsettled as

to the effect of moisture, but corresponds to the results obtained in the study of moisture effects.

D. The Effects of Acidity and Alkalinity of the Food

Normally the reaction of food at the time of putting it in the bottles is acid, the degree of acidity depending upon the length of time it has been fermenting. This sourness usually passes gradually away as the larvæ grow older, and by the time a brood begins to hatch the reaction is frequently quite alkaline, unless fresh food has been put recently into the bottle.

On the other hand, if the acidity of the food is neutralized at the beginning with sodium hydrate or carbonate, or if the reaction is made alkaline while yet there remains a good deal of unfermented banana, the acidity will return for a time if not carefully guarded against. Therefore to keep the reaction acid or alkaline is a difficult matter, and requires occasional stirring of the food to make the reaction uniform; this operation is likely to prove disastrous for the developing pupæ.

In the tests here recorded I used food that had been fermenting for one month, so that it had a very acid reaction that lasted till hatching time. For studies of the effect of alkalinity I used food that had been fermenting about one day and mixed with it sodium carbonate, sodium hydrate or ammonia. The results were unsatisfactory and the reaction did not remain constant in spite of my efforts, though on the whole it remained alkaline, and became strongly alkaline, and also slimy towards the end of the experiment, and not a great many flies hatched.

I also used food that had not been allowed to ferment at all, and although I do not know its reaction, it was certainly not so alkaline as the last mentioned, nor so acid as the first. It was soon attacked by mold (Bread mold). I refer to it here as fresh food.

The results are given in Table XXXI, but may be more briefly summarized here.

Of 483 flies raised on sour food, 17 per cent. were Beaded.
Of 605 flies raised on fresh food, 19.3 per cent. were Beaded.
Of 317 flies raised on alkaline food, 38.1 per cent. were Beaded.

In other words, a high percentage of Beadedness came from flies raised on alkaline food, a low percentage from flies raised on acid food, and intermediate amount from flies raised on fresh food.

A careful study of Table XXXI will reveal the curious partial sex-linkage of which I spoke on pages 15 et seq., and here, too, the explanation suggested there seems to apply as in other cases of the sort. It is not a little peculiar that in all of these food tests this phenomenon should have occurred, though I consider this purely a coincidence. In any case, if we can draw any conclusion at all from its appearance, it would only be that the reaction of the food has nothing to do with the occurrence of the phenomenon rather than the reverse.

E. The Effects of Relative Temperatures

No evident effect was produced by rearing the F_1 generation in an ice-chest, but ratios were as varying as when the flies were raised at room temperature. Ratios of 15.4 per cent., 19.2 per cent., 10.3 per cent., 20 per cent. of Beaded offspring are examples of those given by broods raised at low temperatures. The cold does, however, lengthen greatly the larval life and flies were in the case of the brood last mentioned twenty-eight days in hatching. The brood consisted of 312 normal and 77 Beaded-winged flies.

Similar results were obtained in experiments with heat, except that here the larval life was correspondingly shortened and was at times reduced to eight days. It was not found practicable to keep the flies at higher than 30°–33° Centigrade, as they soon died at higher temperatures.

F. The Effects of Darkness

Flies were raised in complete darkness and sister broods in full daylight, but no differences appeared in the offspring. Of 484 flies raised in darkness 30 per cent. had Beaded wings. Of 360 flies raised in the daylight, 29 per cent. had Beaded wings. This experiment seems

to show conclusively that light and darkness do not influence the percentages of Beaded-winged flies.

IV. THE EFFECT OF SELECTION ON THE PRODUCTION OF DIFFERENT TYPES OF BEADEDNESS

Just how much can be accomplished by selection in Beaded stock was one of the first questions that arose. Morgan (1911*a*) describes the origin of pure Beaded stock as having occurred through the selection of Beaded flies in the early generations after its first appearance. He says the first Beaded fly found arose in a culture of *Drosophila* that had been exposed to radium. Mated to his sisters, 1.6 per cent. of the offspring were Beaded. When these Beaded flies were inbred 3 per cent. of the offspring were Beaded. These inbred gave 8.5 per cent. Beaded offspring.

> The same process continued through many generations has finally produced stock that gives in certain cultures nearly 100 per cent. Beaded wings.

In continuing these selection experiments, he says more extreme forms of Beaded wings appeared, and at the time of publishing (March, 1911) he was attempting "to fix some of these extreme variations." While engaged in this work other wing forms arose, most of which are among the best-known mutants of *Drosophila*. Among these are Truncate, Miniature, Rudimentary, Vestigial and Balloon wings, and the Black and Yellow body colors. Most of these forms have been "purified" now and Beadedness never appears in them though it can still be found in Vestigial stock. All of the above-named forms, by the way, with the exception of Truncate and Rudimentary bred true from the start. The Truncate case is not yet published and Rudimentary has proved (Morgan and Tice, 1914) to be due to a single Mendelian factor. The Rudimentary flies were at first self sterile and highly non-viable, and therefore gave peculiar results in breeding tests.

When I first began work with Beaded flies (Sept., 1912) the stock gave 100 per cent. Beaded-winged offspring.

So soon that I did not realize it, nor think to count the generations, I had one stock that gave offspring much more extremely Beaded than the ordinary stock, and this stock is the one on which most of this report is based. About December, 1912, I started one stock bottle to form the basis for a "No selection" test. The parents of this brood were "pure stock Beaded" males and females. The first generation, no normal-winged flies appeared. The generations following were made up by shaking at random from the bottle of the generation before a dozen or two flies into a new bottle.

The second, third and fourth generations gave three normal-winged flies to 325 Beaded. The sixth, 3 normal to 100 Beaded. In later generations I occasionally found normal flies. The stock is in its 27th generation now, the 25th generation having given rise to a large brood of which I counted 541 flies (284 ♀ and 257 ♂), all of which had Beaded wings of a type averaging like those of Figs. 4–6. It is very apparent that the stock is not undergoing any marked change, though I can not guarantee that it would give exactly the same results in other respects as the extreme (selected) Beaded stock that I have used in the linkage tests.

On the other hand, I have not been able thus far to increase the Beadedness of the selected stock beyond a point which it apparently reached many generations ago. The Figs. 1–12 (excepting 2 and 4), which are here reproduced, were made under Dr. Morgan's direction long before I took up the work, and the forms he had drawn then are as extreme as any that I now have.

If this extreme stock be allowed to go without selection for two or three generations, it "reverts" to a less extreme form, from which it can apparently be recovered by one mass selection. I feel confident that in selecting the extreme forms one merely selects a large percentage of individuals that are heterozygous for l, and of course when the stock is not selected for a while, LL forms become relatively more numerous. This would account for all the facts here recorded.

On the other hand, selection for less extreme Beading is also rapidly effective and normal-winged forms appear soon, but this effect soon reaches its limit apparently, and a normal strain or even a strain throwing a high percentage of normals has not yet been obtained. I am not yet certain that it can not be done. I selected in each direction for eleven generations without marked success beyond that here recorded.

V. MUTATION IN BEADED STOCK

A. General Statement

As will be gathered from statements made in the last section, the Beaded stock has been prolific in giving mutations. There has been no especial attempt made to see how many different mutants could be obtained from the stock, and yet a goodly number have appeared. Most of these have been marked types showing little variation and coming out regularly and distinctly in Mendelian proportions in crosses with other types. They have in general bred true from the start without further selection.

A few of these have been of a sort to confuse for a time the study that I have been making, because of their resemblance to certain types of Beaded flies. The criterion in every case as to whether or not a fly was an ordinary Beaded fly or a new "mutant" was its genetic behavior, and the cases to be here described have, with the exception of Stumpy, shown themselves to be due to a single gene conforming in general to those of other well-known mutants of *Drosophila.*

B. Perfect Notched Wings

In the beginning of my work on Beaded wings I thought it might be possible to isolate definite types from the Beaded stock by crossing out to Wild and extracting the F_2 types that appeared; or by back-crossing the F_1 forms to Wild again and extracting new types, etc. Several thousand flies were raised in the hope of accomplishing this, but the "types" found did not breed true, but continued to behave like ordinary Beaded flies, from whose

many original types none were distinguishable. Finally a genuine new "type" appeared, with both wings alike and definitely "notched" (Fig. 13, p. 730). This female which was at sight named Perfect Notched, was mated to Wild. Her ancestry was as follows:

The grandmother came from pure Beaded stock, and the grandfather from Wild stock. Their offspring consisted of 13 Beaded and 69 normal flies.

A Beaded female of this generation was mated to a normal brother and gave 100 Beaded offspring, male and female, and one "perfect notched" female.

This female and her descendants behaved in a very different manner, genetically, than the Beaded stock from which she arose.

She was mated to a Wild male and gave 62 Beaded offspring and 112 normal offspring. Of the Beadeds, 50 were notched in a way resembling the parent and of the 50, 49 were females. Several other peculiar wing types appeared among the remaining 12 Beaded flies of this generation, but did not breed true and were later discarded.

The notched male gave ordinary Beaded and normal offspring and never gave in either the first or later generations any "notched" offspring. He was probably an extreme variant of a common Beaded type (Fig. 4).

Of the normal offspring of the Perfect Notched female four pairs were made up. Seven hundred and forty-nine normal sons and daughters appeared, and no notched.

Of the notched daughters of the perfect notched female, two were mated to normal brothers and two to Wild males. Their progeny was:

	Notched ♀	Notched ♂	Normal ♀	Normal ♂
By normal brothers	53	0	79	69
By wild males	56	0	47	46

Six of the notched females of this generation were mated to normal brothers and gave

Notched ♀	Notched ♂	Normal ♀	Normal ♂
126	0	144	120

At this time, June, it was necessary to leave New York. In traveling, the Perfect Notched stock was lost. Enough

had, however, been done to show definitely the nature of the mutation involved. It is clear that the perfect notched wings owed their appearance to a dominant sex-linked gene, lethal for males. This accounts for the fact that the males are only half as numerous as the females, and none of them notched, while notched and normal females occur in nearly equal numbers. It also accounts for the fact that the normal females of these generations gave no notched offspring.

Other sex-linked lethal genes have appeared from time to time in the crosses of Beaded flies with others, but none of them were dominant, and therefore they made themselves evident only by preventing the development of one half of the males. I have not worked out the inheritance of these cases.

C. Spread Wings

Comment has already been made on the extreme number of wing types that appeared both in the F_1, F_2, and back-cross generations of the cross between Beaded and Vestigial flies. Most of these forms gave results too complex to be analyzed at present. However, among the offspring of a considerable number of the F_1 females there were flies with wings perfectly normal in appearance save that they were held at right angles to the long axis of the body. In all, 60 flies with Spread wings appeared. One of the 60 had wings very slightly Beaded. Some of them were mated together and produced only spread-winged offspring with no sign of Beadedness. Spread-winged males were mated to Pink Black females in order to test the linkage of Spread. (Pink is in the third chromosome group, and Black in the second.) The F_1 generation gave only flies with red eyes, gray bodies and normal wings (neither Spread nor Beaded). In the F_2 generation were Black flies, Gray flies, and Red-eyed flies with normal and with Spread wings, but none of the Pink-eyed flies had Spread wings, though a large number of F_2 Pink normal flies appeared. The Pink-eyed flies were also mated inter se, but no Spread-winged flies appeared in the F_3 generation. This definitely places the gene for

Spread wings in the third chromosome group. Beaded wings have not appeared in the stock bottles of Spread which breeds perfectly true.

D. Stumpy Wings

Recently a new non-lethal sex-linked character has appeared in the offspring of the cross of an F_1 Beaded male to a Wild female. Its nature has not yet been worked out, since only males have thus far appeared. The flies have wings resembling those of Vestigial, save that they are not held at right angles to the body, but in the normal position. Vestigial is not a sex-linked character.

Summary

The character under consideration is that of Beaded wings in *Drosophila ampelophila.* All gradations of form between that of normal wings (Fig. 1) and those shown in Figs. 2 to 12 occur in the stock bottles, though certain selected strains of the stock give no normal-winged offspring.

When a Beaded fly is mated to a fly of a stock not carrying genes for Beadedness in its germ plasm a varying percentage of the F_1 offspring is Beaded. If the male parent is Beaded the majority of the Beaded offspring are usually females; and if the female parent is Beaded, the majority of the Beaded offspring are usually males. A female Beaded fly however gives a larger percentage of Beaded daughters than does a male Beaded fly. This phenomenon is repeated from generation to generation, no matter whether a given Beaded fly has come from a male or female Beaded parent, and this shows that the phenomenon is not caused by a sex-linked gene.

This phenomenon is not caused by non-disjunction of a sex-linked gene, for tests of both the Beaded and Wild stocks showed non-disjunction to be a rare phenomenon. The only explanation suggested was that the male offspring were somewhat influenced to or away from Beadedness by the nature of the cytoplasm that was brought in with the egg, while females were not readily influenced in this way.

A study of the F_2 generation shows that the majority of the normal F_1 offspring differ from the majority of the Beaded F_1 offspring genetically in that normals give fewer Beaded offspring in the F_2 generation than do the Beaded flies.

Beaded wings showed no linkage to any sex-linked character.

Approximately one half of the flies of the F_1 generation of a cross between Beaded flies and flies with characters whose genes were in the second chromosome, showed linkage in the following generation to second chromosome characters, while one half of the flies did not show such linkage. The cases where linkage did not occur gave a slightly lower percentage of Beaded offspring than did those where linkage was present. An explanation of these phenomena is sought in the suggestion that there was in the second chromosome a gene, here called l, that was recessive but that in the heterozygous condition intensified the dominance of another gene, called B′, which was not in the second chromosome. This gene l behaves as a lethal factor preventing the development of any fly that carries it in a homozygous condition.

All of the F_1 offspring of the crosses of Beaded flies by flies with characters caused by genes in the third chromosome showed linkage in the following generation between Beaded wings and the third chromosome characters. This was taken to signify that there was in the third chromosome a non-lethal gene concerned in the development of Beaded wings. This gene was called B′. This gene was shown to be the essential germinal factor in the production of Beaded wings. It is sometimes dominant and sometimes recessive.

The determination as to whether B′ should be dominant or recessive seems to lie in several possibilities: 1st, the nature of the egg cytoplasm; 2d, the presence or absence of the gene l; 3d, the nature of the environmental conditions.

With reference to environmental conditions, it was shown that a larger percentage of the F_1 generation had Beaded wings when the culture was wet than when it was

dry; and more when the food was alkaline than when it was acid. No other environmental factors were discovered which influenced the production of Beaded wings.

Selection of more or less extreme Beaded flies very quickly moves the average Beadedness of the offspring in the direction of the selection, but this selection apparently becomes further ineffective in a very few generations.

Mutation is of very frequent occurrence in the Beaded stock and the new mutants obtained have in most cases shown themselves to be produced under the influence of one normally Mendelizing gene.

I acknowledge with pleasure the kindly interest and suggestions made from time to time by Dr. A. H. Sturtevant and Mr. H. J. Muller. These have been of much assistance to me. My thanks are also especially due to Dr. T. H. Morgan whose advice and criticisms at critical points have never failed to aid in clearing up the situation.

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SHORTER ARTICLES AND CORRESPONDENCE

ON THE PROGRESSIVE INCREASE OF HOMOZYGOSIS BROTHER–SISTER MATINGS

It has been brought to my attention that the note concerning inbreeding, written at the request of Mr. Phineas W. Whiting to add to his paper on "Heredity of Bristles in the Common Greenbottle Fly, *Lucilia Sericata* Meig.," which appeared in the American Naturalist for June, 1914, might be taken to mean that my data had been sent by Dr. E. M. East to Dr. Raymond Pearl by whom it had been published as his own. I wish to make it clear by a statement of the facts herewith that no such interpretation should be placed upon the note. I was seriously ill at the time and did not submit my manuscript to Dr. Castle or Dr. East for revision, as I should ordinarily have done. In that case no doubt, any ambiguity of statement would have been pointed out to me.

Mendel, in his original paper, showed that if equal fertility of all plants in all generations is assumed, and, furthermore, if every plant is always self-fertilized, then in the *n*th generation the ratio of any allelomorphic pair (A,a) would be $2^n - 1$ AA : 2 Aa : $2^n - 1$ aa. This statement was generalized in 1912 by East and Hayes[1] for any number of allelomorphic pairs. "The probable number of homozygotes and any particular class of heterozygotes in any generation r is found by expanding the binomial $[1 + (2^r - 1)]^n$ where n represents the number of character pairs involved. The exponent of the first term gives the number of heterozygous and the exponent of the second term the number of homozygous characters." A little later Jennings independently showed how homozygotes are produced from heterozygotes by self-fertilization.[2]

East and Hayes[3] published no generalized formula for calculating the reduction toward homozygosis through any other type of mating, but that this was thought to be a proper conclusion deducible from the above is shown by the following quotation (p. 21):

[1] U. S. Dept. Agr., Bur. Plant Ind., Bull. No. 243.

[2] Amer. Nat., August, 1912.

[3] *Loc. cit.*

Close selection, of course, tends toward the same end (homozygosis), but not with the rapidity or certainty of self-fertilization.

This idea is further shown by their statements under the heading "Extension of Conclusions to the Animal Kingdom" (pp. 39–43).

A little later Mr. Whiting had occasion to work out the results of random matings of brothers and sisters, in connection with his work at the Bussey Institution. He found that the amount of heterozygosis was reduced one eighth in matings of the F_2 generation and from this concluded that the remaining heterozygosis was reduced one eighth in each succeeding generation, so that in the nth generation the number of matings which would produce at least some heterozygous offspring would be $(7/8)^{n-1}$. He showed these figures to Dr. East, who agreed with the general conclusion (tendency toward homozygosis), but thought that the ratio would not hold for offspring after the F_3 generation. Dr. East, however, after a casual examination was not able to show Mr. Whiting the fallacy in his work and did not go into the matter further.

In the AMERICAN NATURALIST for October, 1913, Dr. Raymond Pearl criticized the extension of the conclusions for self-fertilized plants to the animal kingdom.[4] He applied the figures of Pearson, 1904,[5] for random matings, which show that the relative number of homozygotes and heterozygotes remains constant in a population where all factors of fertility, virility and environment have the same effect upon each individual in each generation. Dr. Pearl's error, as he has since recognized, lies in the fact that in the F_2 generation random mating involves only brothers and sisters, while in all subsequent generations it also involves other relationships.

When I read Dr. Pearl's article in October I naturally wondered why there was such a difference of opinion between Dr. East, Mr. Whiting and Dr. Pearl. Before finishing the article I computed the amount of homozygosis in the F_1 generation as 0 per cent.; in F_2, 50 per cent.; F_3, 50 per cent.; F_4, 62.5 per cent., and F_5, 68.25 per cent. As soon as possible after that I figured other generations until the heterozygosis would be reduced to one half of one per cent. of the maximum of heterozygosis in the

4 East and Hayes, 1912, *loc. cit.*

5 *Phil. Trans. Roy. Soc.* (A), Vol. 203, pp. 59 and 60.

F_1 generation and found that this was accomplished in the F_{25} generation, the amount of heterozygosis in each generation being:

F_6, 75.000 per cent.	F_{13}, 94.312 per cent.	F_{20}, 98.710 per cent.
F_7, 79.687 per cent.	F_{14}, 95.398 per cent.	F_{21}, 98.956 per cent.
F_8, 83.594 per cent.	F_{15}, 96.277 per cent.	F_{22}, 99.155 per cent.
F_9, 86.719 per cent.	F_{16}, 96.988 per cent.	F_{23}, 99.317 per cent.
F_{10}, 89.258 per cent.	F_{17}, 97.563 per cent.	F_{24}, 99.447 per cent.
F_{11}, 91.309 per cent.	F_{18}, 98.029 per cent.	F_{25}, 99.553 per cent.
F_{12}, 92.969 per cent.	F_{19}, 98.405 per cent.	F_{26}, 99.638 per cent.

With the approval of Dr. Castle and Dr. East I prepared to publish these figures.

Shortly after this Dr. Pearl wrote to Dr. East asking for an opinion upon his article. Dr. East, in the meantime, by a method differing from mine, had worked out the ratios independently. Before answering Dr. Pearl's letter, however, Dr. East compared his results with mine. They agreed. Dr. East then wrote to Dr. Pearl, giving a short rebuttal of Dr. Pearl's arguments, enclosing some of his own figures and adding that a student of Dr. Castle's (myself) was thinking of publishing the complete figures. Dr. Pearl immediately acknowledged his mistake and very generously asked if he should wait until I had published my article before he published a correction. Dr. East replied that he could see no reason for delaying the correction and advised me of this reply.

Since it seemed proper for Dr. Pearl to correct his previous article, I decided to withhold my own figures and incorporate them later in a paper bearing also upon other matters. Dr. Pearl's second article came out in the AMERICAN NATURALIST for January, 1914, and this paper together with the third article in the same journal for June, 1914, shows that his work was entirely independent of Dr. East's or my own.

When Mr. Whiting asked me for a note giving the figures showing what might be expected in the way of an automatic increase in homozygosity when brothers were mated with sisters in successive generations, as Mr. Whiting had done with his flies, I naturally was pleased to have him accept my figures as correcting his own, and at the same time give me an opportunity to acknowledge my indebtedness to those who furnished the idea upon which my figures were based.

H. D. FISH

BUSSEY INSTITUTION,
FOREST HILLS, MASS.
August 18, 1914

NOTES AND LITERATURE

MENDELIAN FLUCTUATIONS[1]

When the observed proportions, say of dominants and recessives, in any Mendelian experiment are worked out for small groups, such as individual litters or the seeds on individual plants in individual fruits, considerable fluctuations round the expected proportions may be observed. In the present note the magnitude of these fluctuations is compared with the magnitude to be expected if the fluctuations were the result merely of chances of sampling—corresponding to the fluctuations that would be observed in drawing, say, samples of black balls from a bag containing white and black balls in the proportion of 3 to 1. In so far as there is good agreement, this is additional confirmation of the Mendelian process holding good in its simplest form: if the fluctuation observed is markedly greater than this theory would indicate, some source of disturbance is certainly present, but whether this disturbance arises from irregularities in the distribution of the gametes or merely from extraneous circumstances (varying death-rates or difficulties of sorting) can not, of course, be determined from the data alone. For albinos in individual litters of mice (Darbishire's data), and for numbers of "green" or "wrinkled" in Mr. Bateson and Miss Killby's crosses of peas I find exceedingly good agreement, at least if very small plants are omitted. Lock's data for maize give good agreement for the DR × DR cross, but poor agreement for the DR × RR cross. Some data given me by Miss E. R. Saunders for seed characters in the individual fruits of stocks show rather irregular results. Further comparisons on similar lines would be of interest, especially for the DR × RR cross, for which very few data are available. For the case to afford a good test the sorting should be clear and there should be nothing in the data to suggest differential death rates obviously.

G. U. Y.

[1] "Fluctuations of Sampling in Mendelian Ratios," G. Udny Yule (Proc. Cambridge Phil. Soc., XVII, 425).

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